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Editor

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UNIVERSITY OF MICHIGAN

LATIMERIA AND THE HISTORY OF COELACANTH FISHES*

By BOBB SCHAEFFER†

The coelacanths and the dipnoans or lungfishes, in the course of their history, share the distinction of spanning a longer time interval than any other comparable categories of vertebrates. Although never particularly successful in terms of adaptive radiation or numbers of described genera, both groups have persisted from the Devonian Period to the Recent, an interval of about 300 million years;

Two of the three genera of modern lungfish were discovered and described over a hundred years ago, the third over 70 years ago. The existence of living coelacanths, however, was not known until 1938, when *Latimeria*[1] was caught off the coast of South Africa. Prior to that year, paleontologists believed that the coelacanths had become extinct at the end of the Mesozoic, a conclusion based on the absence of coelacanth remains in Tertiary sediments. The capture of a second living specimen in December 1952, near Madagascar, assigned to the new genus *Malania*,[2] has aroused considerable popular and scientific interest in this ancient and conservative group of fishes.

Origin of the Coelacanths. The coelacanths are regarded as a distinct suborder of bony fishes, included with the suborder Rhipidistia in the order Crossopterygii, or lobe-finned fishes. The rhipidistians, which existed from the Devonian period into the Permian, have a key position in vertebrate evolution since they gave rise to the first land vertebrates, as well as to the coelacanths (FIGURE 1). The crossopterygians and the dipnoans are grouped together in the subclass Choanichthyes, which is separated from the other major group of higher bony fishes, the Actinopterygii or ray-finned fishes, by a number of well-defined characters including the presence of internal nostrils or choanae in the roof of the mouth. The nasal cavity, with both external and internal nostrils, was probably employed by the choanate fishes for olfactory sampling of the environment rather than for aerial breathing.[3] This arrangement was taken over from the rhipidistians by the first land dwellers for aerial respiration. Internal nostrils have not been discovered in the coelacanth fishes, and they may have been lost during the rhipidistian-coelacanth transition.

Perhaps the most convincing link between the rhipidistians and the Devonian coelacanths is the structure of the braincase (FIGURE 2). In both, it is ossified in two parts which are joined by a sort of hinge joint. A slight amount of motion may have occurred between them—probably a shock-absorbing mechanism associated with jaw movement. There is some evidence that the early Devonian lungfish and even the first actinopterygians, had a similar sort of kinetic arrangement[4] in the braincase, derived from a common, but still unknown, ancestral stock for all the higher bony fishes.

In both the rhipidistians and the Devonian coelacanths, the palate articulated with the basipterygoid process, a projection extending laterally from the base of the braincase. The first known coelacanths, however, had already developed an additional connection with the upper part of the braincase.

The dermal-bone covering of the skull was considerably modified during the transitional period. The maxillary bone, an important tooth-bearing element in the upper jaw of the rhipidistians, was lost. The parietal bones (or more probably the post-parietals) were apparently also lost, with the laterally adjacent intertemporals replacing them along the midline of the skull roof. Certain dermal bones in the cheek area disappeared, and others apparently shifted their positions. The number of supraorbital bones increased and the sensory canal, which in the rhipidistians ran through the bones of the skull roof, shifted laterally to a position between the supraorbitals and the frontonasal series. The lower jaw was modified from the rhipidistian type with the shortening of the tooth-bearing dentary bone, the elongation of the angular bone and enlargement of the coronoid bone. The dentition became generally weaker, but had about the same distribution as in the rhipidistians.

These changes in the skull resulted in a structural pattern that is peculiar to the coelacanths. Although the functional meaning of the altera-

* This paper, illustrated with lantern slides, was presented at a meeting of the Section on March 2, 1953.

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tions is obscure, many or most of them were probably interrelated. Certain modifications indicate a change in the jaw mechanism. It might be mentioned here that the stomach of *Malania* contained skeletal remains of bony fishes, indicating that the living coelacanths are predators. Probably most of the fossil forms were also predaceous, as were the rhipidistians.

The crossopterygians have a cartilaginous notochord extending from the skull into the caudal fin (FIGURE 3). In the rhipidistians it is usually surrounded by bony ring-shaped intercentra. These are missing in the coelacanths. The coelacanths retained the short dorsal ribs of their ancestors.

The pectoral girdle is narrower in the coelacanths than in the rhipidistians. It lost one ossification

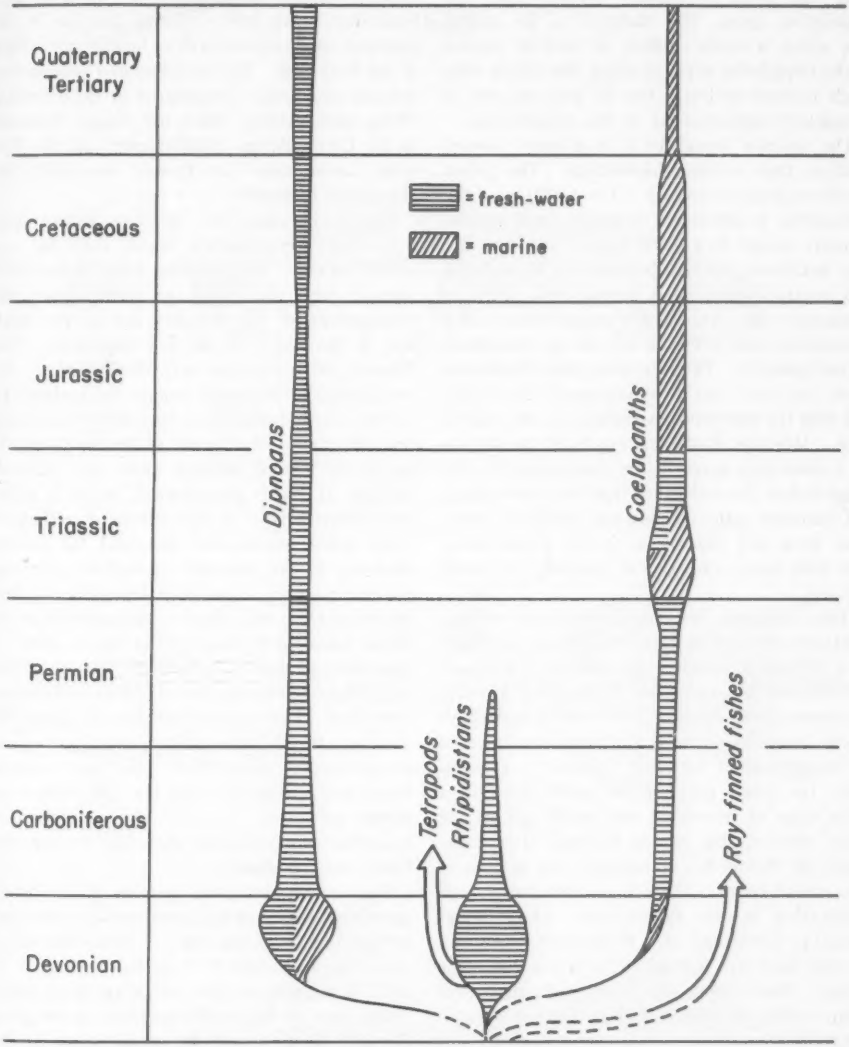

FIGURE 1. Phylogeny of the choanate fishes

(the interclavicle and gained another (the extracleithrum). With one or two exceptions, the pelvic girdle of the coelacanths is of characteristic form and could be readily derived from the rhipidistian type. The skeleton of the paired fins, which is rarely ossified, is basically similar to the rhipidistian type, although the radials were much reduced or lost. The fin rays are not as completely segmented as in the rhipidistians.

The anterior dorsal fin is in a more forward position than in the rhipidistians. The pelvic fin also migrated anteriorly. The caudal fin of the coelacanths is distinctive in that a small supplementary caudal fin projects beyond the main fin. The notochord, running between the large dorsal and ventral caudal lobes, extends into the supplementary fin. The earliest rhipidistians had a heterocercal tail with the end of the notochord turned upwards. The Devonian genus *Eusthenopteron*, however, has a symmetrical three-lobed tail with the notochord extending into the middle lobe. Although *Eusthenopteron* lived too late to be a coelacanth ancestor, the structure of its tail suggests how the coelacanth type may have arisen.

Coelacanth scales are thin and cycloidal, rather than thick and rhombic as in the rhipidistians. One scale layer, consisting of cosmine, was much reduced.

The coelacanth body is generally shorter and relatively deeper than in the rhipidistian ancestors. It is difficult to correlate the changes in the postcranial skeleton and in body form with differences in swimming mechanics. The over-all coelacanth design indicates powerful but not normally rapid swimming except for short distances. Presumably, the lobate pectoral and pelvic fins had a wide range of movement and could support the body when resting on the bottom. The coelacanth air bladder has an ossified wall, at least in the extinct forms. There is no evidence of such ossification in the rhipidistians. The bladder probably functioned as a hydrostatic organ and it may have had a respiratory function in some forms. Observations on living coelacanths will help to clear up many of these functional problems.

Post-Devonian History. Following their origin in the early or middle Devonian, the coelacanths became exceedingly conservative in their rate and degree of evolutionary change. Although various genera show modifications of the basic coelacanth design, these innovations apparently established no evolutionary lines that can be traced through a succession of genera.

The important long-range, post-Devonian changes occurred in the skull. By the early Carboniferous, there was a marked decrease in the degree of ossification as well as further subdivision of the braincase. The basipterygoid process was reduced and finally disappeared in the Permian. These modifications, which are clearly indicated in the Carboniferous *Rhabdoderma*[5] and the Permian *Coelacanthus*[6] are present essentially unchanged in *Latimeria*.

Certain Permian and Mesozoic genera have interesting specializations which may be considered briefly. The Permian form *Spermatodus*[7] shows convergence toward the rhipidistians in the arrangement of the dermal-bones of the cheek and in the angle of the jaw suspension. The Triassic period was apparently the time of greatest morphological divergence among the coelacanths. In the Triassic *Laugia*[8] and *Piveteauia*[9] the pectoral fins were raised on the side of the body and the pelvic fins moved forward under the pectorals (FIGURE 4). This arrangement, which is otherwise characteristic of the advanced actinopterygian fishes, presumably increased the braking efficiency of the pectorals as well as swimming maneuverability. Among the Triassic genera from Spitzbergen[10] *Axelia* shows a degeneration of the cheek bones and *Scleracanthus* has a dentition apparently adapted for crushing. The late Triassic *Diplurus*[11] has long, ossified ribs and a shortened lower jaw. The conservative Jurassic genus *Undina* and the Cretaceous *Macropoma* seem to be closely related. The cheek bones have a similar shape and arrangement and are well ossified and closely associated. In both, the supplementary caudal fin is reduced and the other fins are more lobate than pedunculate.

Latimeria is a typical member of the Coelacanthini as far as can be determined from the single mounted specimen (FIGURE 5). It has been placed in a separate family [12, 13] mainly because of the form of the pectoral fins, which are more pedunculate than in the earlier members of the group. Actually all the fins of this genus except the first dorsal fin are unusually developed in this respect, but the pedunculation is a matter of degree, and perhaps is not of major importance. The skull pattern of *Latimeria* is more suggestive of certain Triassic genera than of the known Jurassic or Cretaceous forms. On the basis of present knowl-

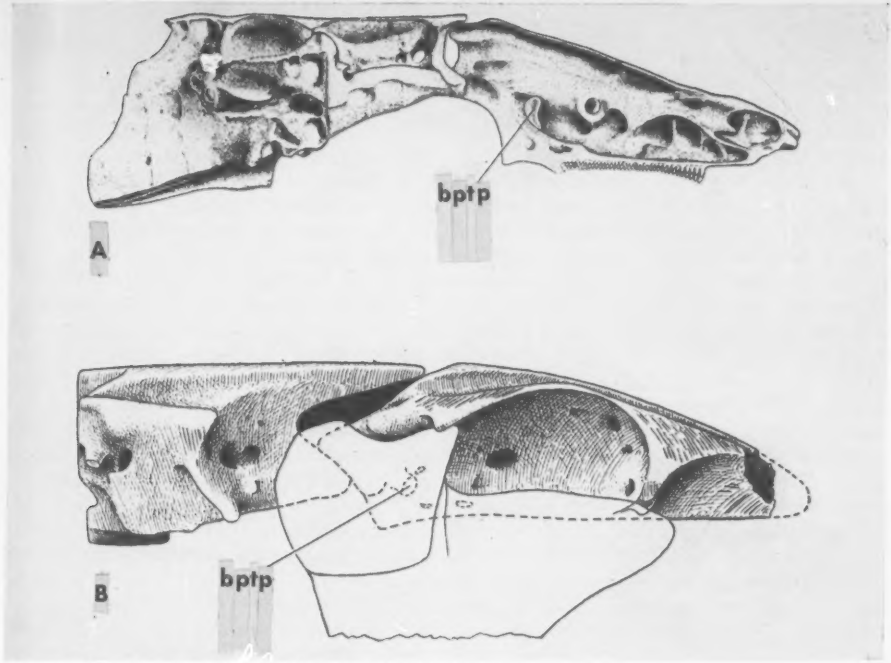

FIGURE 2. Comparison of rhipidistian and Devonian coelacanth braincases.
A. Early Permian rhipidistian *Ectosteorhachis* (after Romer).
B. Late Devonian coelacanth *Diplocercides* with palate in position (after Stensiö). (bptp = basipterygoid process).

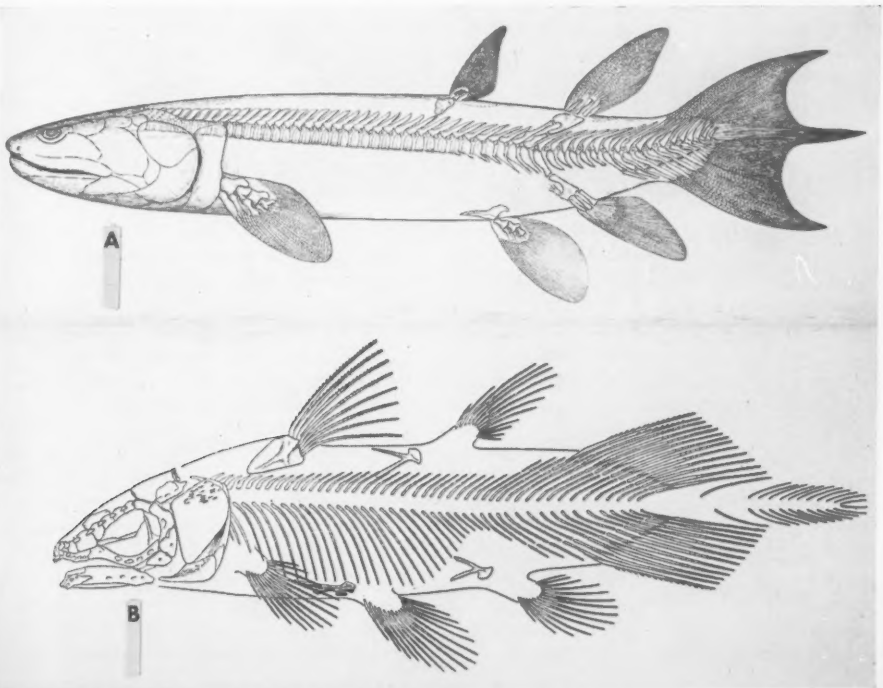

FIGURE 3. Comparison of two main types of crossopterygian skeletons.

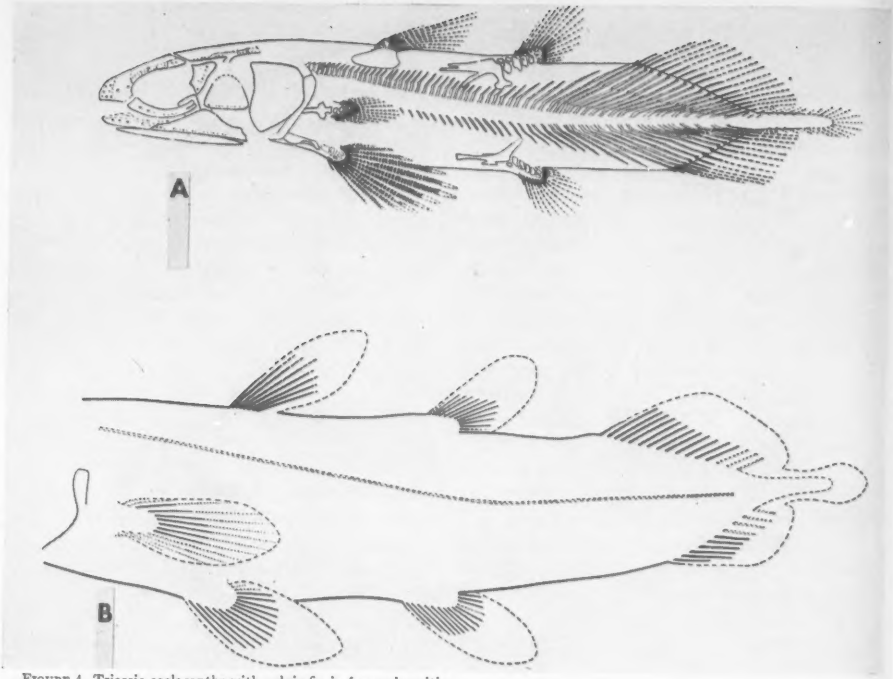

FIGURE 4. Triassic coelacanths with pelvic fin in forward position.
A. *Laugia* (after Stensiö).
B. *Piveteauia* (after Lehman).

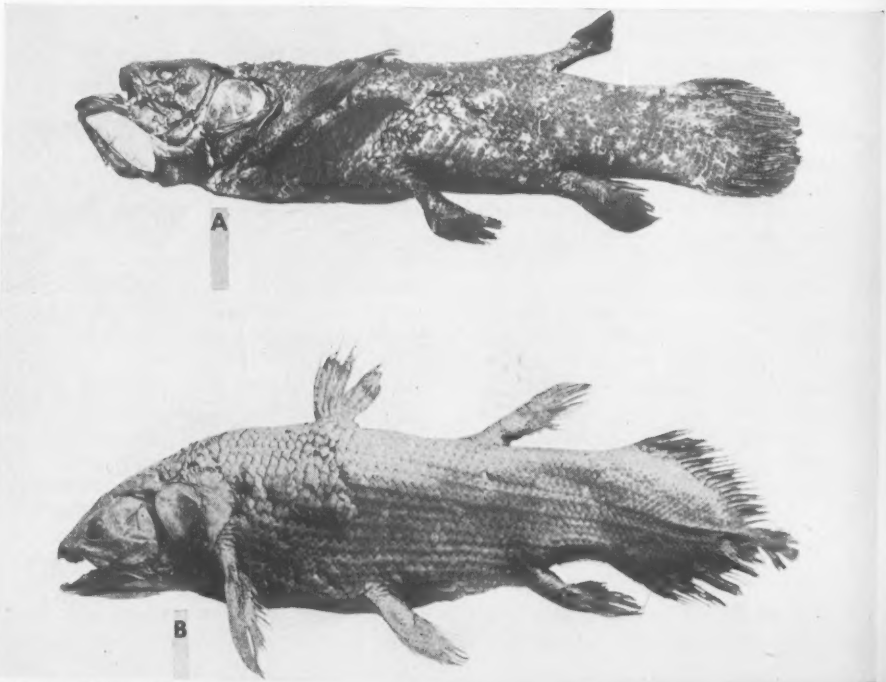

FIGURE 5. Living coelacanths.
A. *Malania* (courtesy of Life).

edge, it is not possible to regard any described Mesozoic genus as a direct ancestor of this living genus.

Until *Malania* has been fully described, some doubt will remain concerning the validity of a separate generic designation. The supplementary caudal fin of this specimen is missing, and the main caudal fin is differently shaped than in *Latimeria* (FIGURE 5). Whether the absence of the supplementary caudal is normal, pathological, or due to the action of some predator early in life remains to be determined. If normal for this genus, it is a unique condition among known coelacanths, perhaps representing a character of family rank. The loss of the first dorsal fin is obviously the result of predator action since the basal plate is present, and scar tissue is developed where the fin should be.[3] Since the specimen of *Malania* is nearly complete, it will supply important information on the soft anatomy of coelacanths in general. Perhaps the arrangement of the muscles and the structure of certain other parts of the body will aid in the interpretation of rhipidistian anatomy. It must be remembered, however, that the living coelacanths are marine forms, separated by a long time interval from their rhipidistian ancestors.

Coelacanth Environments. Most living fossils, such as the lingulids, sphenodontids and the opossums, have inhabited essentially the same basic environment since the time when they first appeared in the fossil record. The dipnoans had a marine invasion in the Devonian, but after that time they have always lived in streams and fresh water swamps. The coelacanths are perhaps unique in that they have invaded a number of different aquatic environments during the course of their history—ponds, lakes, streams, coal-swamps, shallow epicontinental seas and probably during most of the Cenozoic, the continental shelves bordering the open sea.

Like the Devonian dipnoans, the coelacanths of that period were both marine and fresh-water dwellers. The middle and late Devonian forms from the Rhine Valley[14] are found in rocks of marine origin. An undescribed coelacanth has been collected in fresh-water upper Devonian beds in eastern Canada[15] and another has been described from beds of the same age in Spitzbergen (the genus *Dictyonosteus*, formerly regarded as a rhipidistian[10]). Since the rhipidistians were an exclusively fresh-water group, it is probable but by no means certain that the coelacanths had a fresh-water origin followed by a Devonian invasion of the sea. All the known Carboniferous and Permian genera are found in rocks of fresh-water origin and many of the deposits indicate swampy conditions.[5]

About 40 per cent of the known Triassic genera were fresh-water inhabitants, the remainder brackish-water or marine. This evidence might suggest a return to the sea early in the Mesozoic, but it is also possible that the coelacanths continuously occupied marine habitats throughout the Carboniferous, along with one or more fresh-water invasions.

The other Mesozoic genera were all marine, as are the living representatives. The failure to discover coelacanth remains in Tertiary sediments may be related to a greatly restricted range during most of this period as well as to the slight chance for preservation. *Latimeria* and *Malania* are apparently offshore fishes, occurring in areas along the east African coast and around Madagascar that are seldom trawled. Once their habitats have been determined, they may turn out to be fairly common.

Rates of Evolution. The various types of evolutionary rates and the methods of determining them have been discussed by Simpson[16, 17, 18] and will not be considered here. There are two general sorts of rates, morphologic and taxonomic, which may be worked out on the basis of the fossil record. Most morphologic rates require a rather complete fossil lineage for a given group of organisms, permitting measurements of some character through a series of geologically successive genera. These measurements are then converted to logarithms or some other appropriate form and plotted against time in terms of millions of years.

The present impossibility of working out evolutionary lines in such groups as the coelacanths and lungfishes makes it necessary to employ another method in determining a morphologic rate. Following Westoll[19] it is possible to arrange a series of successive coelacanth genera which demonstrate the major, suprageneric changes that have occurred in the entire group through time. Beginning with the relatively radical alterations during the rhipidistian-coelacanth transition, the changes are listed according to subdivisions of the skeleton (braincase, skull roof, cheek area, paired fins, etc.). A morphologic rate is then determined by counting the number of structural changes per million years for a time interval either between the approximate first appearances of two successive genera or for a

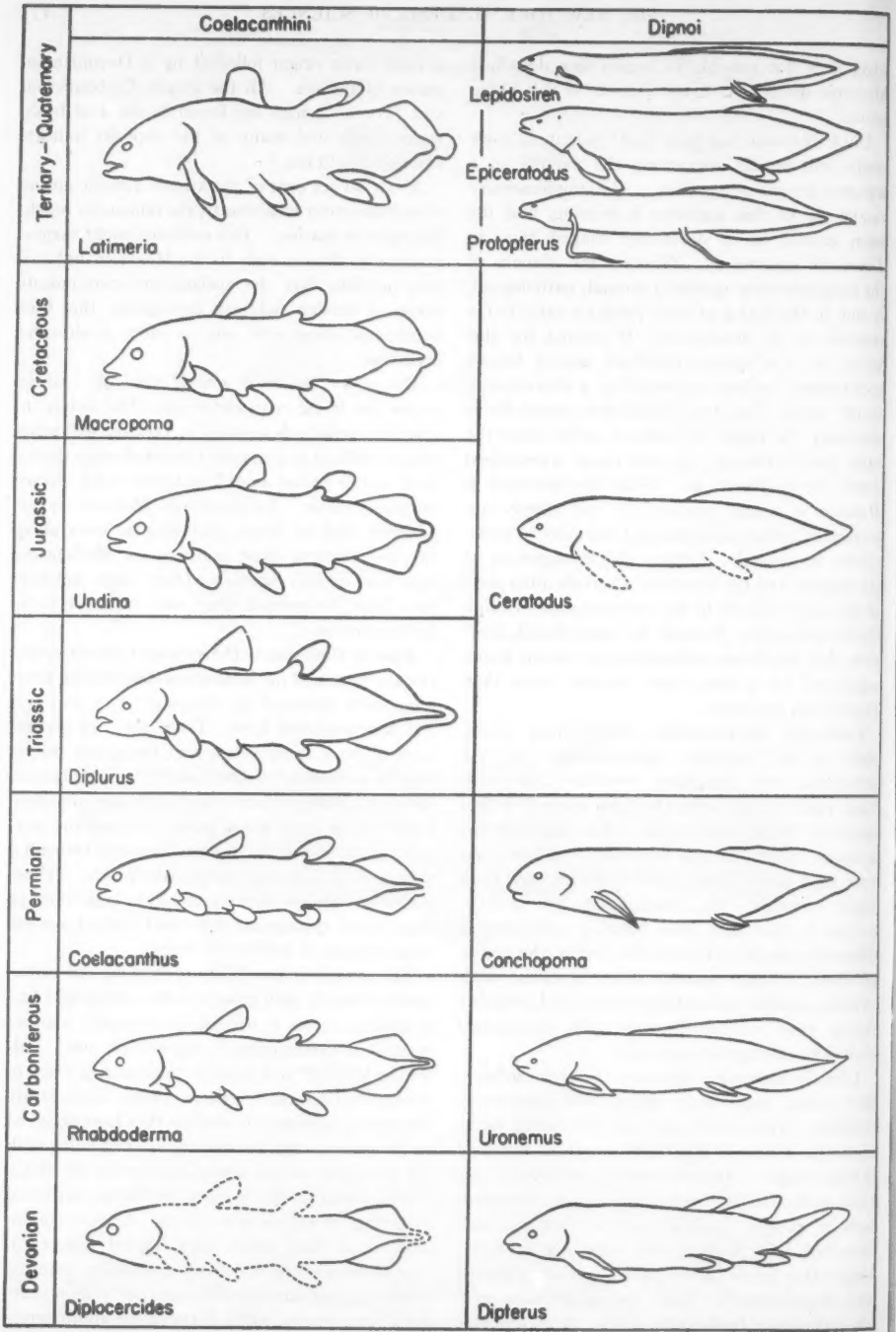

FIGURE 6. Representative coelacanth and dipnoan genera for each of the geologic periods in which these groups occur. *Latimeria* is unknown in the Tertiary.

period including the ranges of several genera that show the same modification. Strictly generic characters are not considered.*

Since rate curves of this sort have little meaning when considered separately, the coelacanth curve is compared with a dipnoan curve derived from Westoll's data (FIGURE 7). Both curves show a marked rise in rate during the transitional period, presumably correlated with a change in adaptive zones and with the successful occupation of available ecologic niches. The rapid decline and subsequent leveling off of the rate curves was probably associated with the observed stabilization of suprageneric structural patterns in both groups. Failure to compete successfully with the rapidly

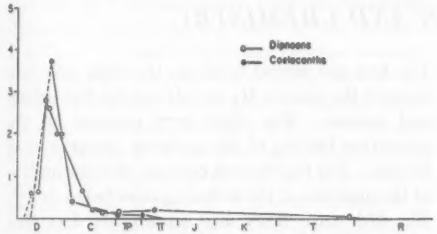

FIGURE 7. Rate of acquisition and subsequent modification of suprageneric morphologic characters in the coelacanths and dipnoans.

evolving and radiating actinopterygian fishes undoubtedly brought about the elimination of the coelacanths in fresh-water during the Triassic period, and narrowed the environment available to the dipnoans.

The type of taxonomic rate that can be most readily worked out for the coelacanths, dipnoans and for the major groups of actinopterygian fishes is called an origination rate.[18] It is based on the number of new genera per million years (FIGURE 8). Although minor fluctuations in the curves are partly related to record deficiencies and taxonomic difficulties, it is evident that the taxonomic rate for the choanate fishes has been generally low throughout their history. The curves for the actinopterygian groups present a quite different picture, with a much higher rate of diversification, particularly for the teleost fishes.

Although the morphologic and taxonomic rates cannot be compared directly since they are based on different sorts of data, it is evident that the former expresses the tempo of structural change for the entire group, while the latter represents the rate of morphologic and taxonomic change at the generic level. Both show the slow evolutionary pattern characteristic of the coelacanths and the dipnoans from the time of their first appearance in the fossil record to the present time.

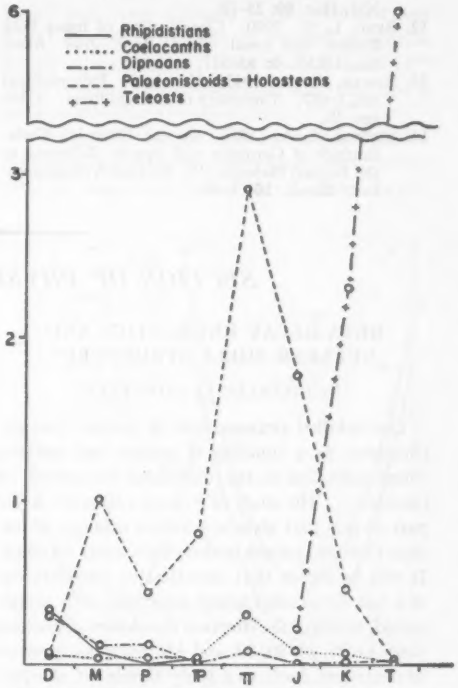

FIGURE 8. Origination rate of new genera per million years for various groups of higher bony fishes.

*Further details of this method and its limitations are considered elsewhere.[11, 19, 20]

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SECTION OF PHYSICS AND CHEMISTRY

BETA-DECAY ENERGETICS AND NUCLEAR SHELL STRUCTURE*

By CHARLES D. CORYELL†

The detailed consideration of nuclear thermochemistry as a function of proton and neutron composition lies in the traditional framework of chemistry. The study of β-decay energetics is one part of this that gives a sensitive measure of nuclear chemical factors underlying nuclear stability. It will be shown that quantitative consideration of a few factors in nuclear structure, with proper consideration of the effects of the closure of nucleon shells at 20, 28, 50, 82, and 126 nucleons (protons or neutrons), leads to a fairly simple set of equations predicting β-decay energetics of all nuclei from mass number 50 to 250. The uncertainty of the predicted values is about 0.2 Mev for odd-A nuclides and about 0.5 Mev for even-A nuclides.

About two decades ago, the main features of nuclear energetics, apart from the effects of shell structure, were established with the liquid drop model (W. Heisenberg, G. Gamow, C. von Weizsäcker, N. Bohr, J. A. Wheeler). According to this statistical picture, the mass M of a nuclide of charge Z and mass (nucleon) number A may be given for $A > 50$ as:

$$M(Z,A) = ZM_H + (A-Z)M_n - a_1A + a_2A^{2/3} + a_3\frac{(A/2-Z)^2}{A} + \frac{3}{5}\frac{Z^2e^2}{r_0A^{1/3}} + \text{pairing term} \quad (1)$$

The first and second terms on the right take into account the masses M_H and M_n of the free proton and neutron. The third term corrects for the saturation binding of the nucleons, irrespective of nature. The fourth term corrects for unsaturation of the nucleons at the surface, proportional to $A^{2/3}$. The fifth term takes into account the fact that neutron-proton pairs contribute more to the binding than excess of either, assuming a quadratic in $A/2 - Z$. The sixth term takes into account the coulombic destabilization of the nucleus, taking the radius R as $r_0A^{1/3}$, where r_0 is calibrated from α decay, from β-decay energetics of mirror nuclei which undergo β-decay without change in number of neutron-proton pairs, and from nuclear scattering cross sections. The last term takes into account the fact that protons or neutrons pair as far as possible; there should be a mass increment $\delta_A/2$, dependent on A, when either the number of protons Z or the number of neutrons N is odd. The pairing term thus was given the values $+\delta_A$ for Z odd A even, 0 for Z even and A even, and $+\delta_A/2$ for A odd (Z or N odd).

Equation (1) is quadratic in Z at constant A, and may be transformed to energy scale E and simplified for isobaric sequences as:

$$E(Z,A) = E(Z_A,A) + \frac{B_A}{2}(Z_A - Z)^2 \pm \delta_A/2 \text{ or } 0 \quad (2)$$

where Z_A is the (non-integral) charge corresponding to the vertex of the energy parabola, B_A is its curvature, and the pairing term leads to $+\delta_A/2$ for odd Z even A, $-\delta_A/2$ for even Z even A, and

* This paper, illustrated with lantern slides, was presented at a meeting of the Section on March 3, 1953. The work reported here was supported, in part, by the U. S. Atomic Energy Commission.
† Department of Chemistry and Laboratory for Nuclear Science, Massachusetts Institute of Technology.

0 for odd A. Correlation of equation (1) and equation (2) shows that:

$$Z_A = \frac{(M_n - M_H + a_3)A}{2a_3 + 6e^2A^{2/3}/5r_0} \quad (3)$$

$$B_A = \frac{M_n - M_H + a_3}{Z_A} \quad (4)$$

The parabolic dependence of energy on charge required by equation (2) is shown in FIGURE 1, with parametric Z_A and B_A values for $A = 133$ and $A = 134$. Decay by negatron (β^-) emission will occur when $E(Z, A)$ is greater than $E(Z + 1, A)$. Its converse, electron capture, will occur if $E(Z_A, A)$ is greater than $E(Z - 1, A)$. Positron (β^+) emission may occur if this energy difference exceeds the rest mass of two electrons (1.02 Mev), recoverable as annihilation radiation (two γ rays) when the positron has been slowed down. Computed β^- or electron-capture decay energies are given in FIGURE 1 in Mev. The total β decay energy Q^β in decay is that between ground states, including energy of γ radiation following β emission and energy of isomeric transition of daughter, if one is formed. For convenience, we shall consider decay only in the direction $Z \rightarrow Z + 1$, and express the electron capture energy Q^C of the nuclide $(Z + 1, A)$ as a negative Q^β for (Z, A). From equation (2) it may be seen that:

$$Q^\beta(Z, A) = -Q^C(Z + 1, A)$$
$$= B_A(Z_A - Z - 0.5) + \text{pairing term} \quad (5)$$

where the pairing term is $+\delta_A$ for odd Z even A, $-\delta_A$ for even Z even A, and 0 for odd A.

A consequence of the equation (2) is that only one nuclide of given A should be stable to electron capture if the pairing term is zero (odd-A), namely that which has Z within the limits of $Z_A \pm 0.5$. Such a species is called β-stable. Instability to α emission is less decisive, high α-emission energies occurring for high Z species because of the increasing weight of the coulombic term in equation (1). For even-A species, there may be two or even three β-stable species, all with Z even (see FIGURE 1). All but one of these may be metastable to decay by double β emission or double electron capture, very improbable processes.

Detailed evaluation of the parameters for equation (1) or (2) has been carried out by a number of workers, as discussed in a recent review.[1] One of the most widely accepted set of parameters is that of Fermi,[2] who took r_0 as 1.48×10^{-13} and established the value of 0.083 for a_3 (atomic mass units) in equation (1) from a consideration of the occurrence of β-stable odd-A nuclides. This value of a_3 corresponds by equation (4) to the value 78.0 Mev/Z_A for B_A. The values of a_1 and a_2 that Fermi took from absolute masses (0.01504 and 0.014) are not of concern in β-decay energetics. Fermi[2] estimated the pairing term δ_A as $67/A^{3/4}$ Mev; evidence will be presented later that this is not an appropriate representation.

More detailed studies have shown that equation (1) and its specializations for β-decay, equation (2) with the simple function (3) for Z_A failed to correlate with detailed properties of nuclei. Many authors, including Bohr and Wheeler,[3] Feenberg,[4] and Kohman,[5] have sought local solutions for Z_A, and represent the parabolic "valley of stability" as a winding one. Developments of the last few years have shown that the main part of deviations from the simple pattern are associated with closure of nucleon shells, with predictable effects on the Z_A function and identifiable influence on the pairing terms.

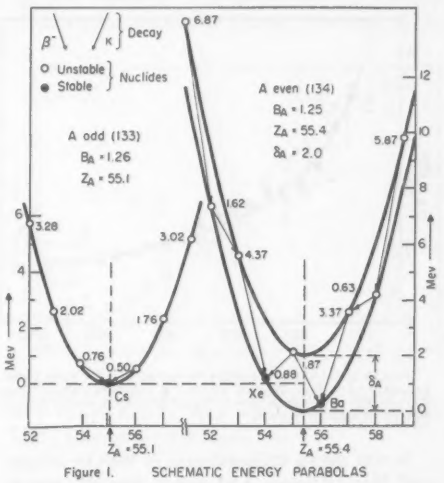

Figure 1. SCHEMATIC ENERGY PARABOLAS

FIGURE 1. Schematic Energy Parabolas. Energy versus charge, odd-A species left side, even-A species right side.

Simple consideration of the potential function for nucleons, in between a square well and a parabolic well,[6] indicates that the order of filling of quantum levels in either neutrons or protons should be:

$1s, 1p, 1d, 2s, 1f, 2p, 1g, 2d, 3s, 1h, 2f, 3p, 1i$, etc. (6)

where the letters s, p, d, f, etc. refer to values of l, the orbital quantum numbers of 0, 1, 2, 3, etc., and the numbers designate number of radial nodes plus one.

The protons or neutrons (of spin ½) separately fill the levels, joining in pairs as far as possible. The total angular momentum j of a nucleus with an unpaired nucleon may be $l + ½$ or $l - ½$. The population of a quantum level is $4l + 2$. Breaks in energy spacing are expected at the filling of the $1s$ (2 nucleons), $1p$ (total of 8 nucleons) and $1d + 2s$ (20 nucleons). Further breaks observed (28, 50, 82, 126) are not in accord with the filling of the quantum levels listed above.

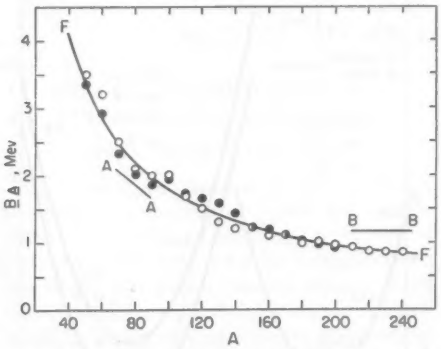

FIGURE 2. Curvature B_A of the Parabolas. Line FF from Fermi parameters;[3] ○ Bohr-Wheeler values;[3] ● Feenberg values;[4] lines AA and BB local solutions.[13, 14] Figure by permission of Annual Review of Nuclear Science.

It was shown independently in 1949 by Mayer[7] and Haxel, Jensen, and Suess[8] that the key to clarification of nuclear structure is the assumption that a strong spin-orbit coupling exists, whereby for large l the state with $j = l + ½$ is more stable than that with $j = l - ½$ by about 2 Mev. There can be $2l + 2$ nucleons with $j = l + ½$, and $2l$ with $j = l - ½$.

Shells mark the occurrence of gaps in a sequence of energy levels. Accordingly a shell occurs when the $1f_{7/2}$ level is filled with 8 nucleons (28 total), after which the $1f_{5/2}$ level fills. The spin-orbit effect throws this up close to the energy region of $2p_{3/2}$ and $2p_{1/2}$, and the same effect with $1g$ throws the $1g_{9/2}$ down to the same energy region. The next pronounced gap due to spin-orbit coupling is due to the break at 50 nucleons on going from $1g_{9/2}$ to $1g_{7/2}$. The shell-number 82 comes from the break between $1h_{11/2}$ and $1h_{9/2}$, and the number 126 comes from the break between $1i_{13/2}$ and $1i_{11/2}$.

Besides corroboration from the data on β-energetics covered below, the shell picture has been corroborated by considerations of binding energies, identifiable quantum numbers from transition probabilities, magnetic moments of species with odd nucleons, and quadrupole moments.[7, 8] Indeed, the quantum properties of a nucleus are generally predictable from the properties of the odd nucleons established from the energy sequence given above (single particle model).

In all correlations of nuclear properties such as decay energies, it is necessary to segregate data for the various shell regions, and it is also desirable to look for the possibility of other smaller energy breaks that might be expected from the sequence given, as 34 for the $1f_{5/2}$—$2p_{3/2}$ break, 64 for the $2d_{5/2}$—$2d_{3/2}$ break, and 100 for the $2f_{7/2}$—$2f_{5/2}$ break.

It is easy to see the effects of spin-orbit energy breaks on β-decay energetics. Equation (5) is found to be quite adequate to represent decay energies inside a region of given proton and neutron shells, with Z_A taken as an empirical smooth function of A. For simplicity, data will be considered first only for A odd, and Z either always even or odd. The β-decay process can also be represented as the consequence of evaporating a neutron from the nucleus (Z, A), on supplying energy equal to the binding energy of a neutron $B^n(Z, A)$, permitting the neutron to decay with energy release $M_n - M_H = 0.78$ Mev, and condensation of the proton on the nucleus with binding energy release $B^p(Z + 1, A)$. The correlation of the two processes for Q^β is:

$$Q^\beta = B^p(Z + 1, A) - B^n(Z, A) + 0.78 = B_A(Z_A - Z - 0.5) \quad (7)$$

In a given shell region B^p and B^n are smooth functions of composition (Z, A) reflected in smoothness in the right term of equation (7). If the composition sequence crosses a shell number for neutrons, B^n suffers a downward discontinuity of about 2 Mev and Q^β suffers an upward discontinuity in the same amount. This must be accompanied by a discontinuity in the term on the right. Experiment shows that it is not carried by B_A, so it must be accompanied by a change in Z_A, with $B_A \Delta Z_A$ being 2 Mev. Correspondingly crossing a proton shell number causes a drop in Q^β and in Z_A in the same manner. These effects were identified by Brightsen[13] and independently by Suess and Jensen.[11] A detailed evaluation will

be presented after the shell effect on pairing terms is treated.

By plotting β-decay energies of odd-A nuclides for sets governed by simple functions of Z and N against Z or N, it is easy to show that the pairing term is in some shell regions different for odd Z than for odd N. This was pointed out by Glueckauf[9] and by Suess.[10] In a comprehensive study, Suess and Jensen[11] established the fact that this effect is shell-regulated, although there is as yet no theoretical explanation for it.[12] The presently available data have been reviewed by Coryell.[1] Identifying an instability term π for an odd proton and ν for an odd neutron, the decay of an odd-Z odd-A species will differ by $(2\pi - \nu) = 2\epsilon_A$ from the value interpolated from neighboring even-Z odd-A species. Numerical values of $\pi - \nu = \epsilon_A$ are given[1] in TABLE 1.

TABLE 1

PAIRING TERMS FOR β-DECAY OF ODD-A NUCLIDES

Shell Region	ϵ_A(Mev)	Decay Energy Increased	Decay Energy Decreased
$Z \geq 28$	−0.3	Ni, Zn, Ge(½)	Cu, Ga
$N > 50$	+0.4	Rb, Y, Nb, Tc	Kr, Sr, Zr, Mo, Ru(½)
$N > 82$	+0.35	Cs, La, Pr, Pm	Xe, Ba, Ce, Nd, Sm(½)
$Z \geq 82$, $N \geq 126$	+0.16	Bi . . . Am	Pb . . . Cm

What is singular about the departure of ϵ_A from zero is its abrupt onset on crossing the shell edges noted in TABLE 1, and its rather sudden disappearance after the new shell sequence is started. The effect occurs for only those isotopes of the elements listed whose neutron composition satisfies the requirements of column 1. The symbol (½) in TABLE 1 implies that $\frac{1}{2}\epsilon_A$ is to be used for the β^--decay of the element so identified; for higher Z values, ϵ_A seems to be zero.

Within the shell regions the evidence is fairly good for parabolic dependence of $E(Z, A)$ on Z, and as yet there is no evidence that the curvature of the parabola B_A suffers appreciable discontinuity on crossing shell edges. Data from several sources is included in FIGURE 2, taken from the author's detailed review.[1] The line FF is based on the Fermi parameter a_3.[2] Data from local solutions of Bohr and Wheeler[3] and Feenberg[4] are designated by open and closed circles. The line AA represents the average value for B_A obtained by Brightsen[13] for $N \leq 50$, and the line BB represents the average value for B_A, 1.16 ± 0.16 Mev obtained by Coryell and coworkers[14] for the heavy element region, $208 < A < 245$. Uncertainties in B_A seem to be of the order of 10 per cent. In the absence of better evidence, B_A will be taken from line FF in FIGURE 2 up to mass number 180, after which it will be taken as constant at 1.16 Mev.

Having identified the B_A and the ϵ_A functions, Z_A values can be evaluated from observed β decay energies by a modification of equation (5):

$$Z_A = \frac{Q^\beta}{B_A} + Z + 0.5 \pm \frac{\epsilon_A}{B_A} \qquad (8)$$

where the plus sign in the last term is taken for Z even and the minus sign for Z odd, with values of ϵ_A from TABLE 1. The condition for β stability of an odd-A nuclide of charge Z is that Z_A lie

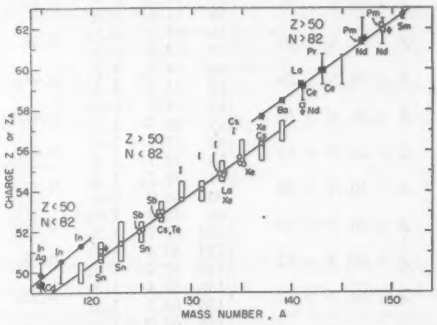

FIGURE 3. Analysis for Z_A as a Function of A. I or □, stable odd-A nuclides. ●, ○ Z_A from β^- decay and □ Z_A from positron emission, elements decaying indicated near curve. Figure by permission of Annual Review of Nuclear Science.

within the region $Z - 0.5 \pm \epsilon_A/B_A$ and $Z + 0.5 \mp \epsilon_A/B_A$, the upper set of signs applying to even Z and the lower to odd Z.

With the aid of these two principles, the course of Z_A can be determined from all reliable β decay data and the existence of stable odd-A nuclides, as illustrated in FIGURE 3 for $115 \leq A \leq 151$ in which three shell regions are represented. The Z_A function for $Z < 50$ is based on data from $A = 87$, and in the whole region Z_A is linear with A with a slope of 0.397. On crossing $Z = 50$, Z_A undergoes a downward discontinuity of 1.2 charge units, or $B_A \Delta Z_A = \Delta B^\nu = -1.9$ Mev. In the next region, Z_A is again linear with A with a slope of 0.350. The absence of $\pi - \nu = \epsilon_A$ effect is shown by the lack of difference in Z_A fit of species of odd and even Z, identified by symbols above and below the curve. On crossing $N = 82$, Z_A undergoes an upward discontinuity of 1.40

charge units, or $B_A\Delta Z_A = -\Delta B^n = +1.9$ Mev. The new Z_A slope is 0.357.

Above $N = 82$ the pronounced ϵ_A effect of TABLE 1 has been taken into account by equation (8), after which unambiguous correlation of Z_A with the observations is attained. The break in Z_A curve at $N = 82$ explains the absence of stable odd-A isotopes of cerium ($Z = 58$), as Ce^{141} and Ce^{143} would be on extensions of the middle region, but since they have $N > 82$ they have higher Z_A corresponding to β instability. The complementary effect at $Z = 50$ provides for three β-stable species of tin (FIGURE 3). A positive value for ϵ_A limits appreciably the stability of odd-Z nuclides. In particular, none occurs for promethium ($Z = 61$) because Z_A reaches 61 very close to an even A number (146). Pm^{145} is unstable to electron capture and Pm^{147} is unstable to β-decay. A similar interaction of positive ϵ_A effect and Z_A striking 43 close to $A = 98$ accounts for the absence of stable technetium isotopes in nature.

TABLE 2

THE SECTIONS OF THE Z_A FUNCTION AND ASSUMED B_A VALUES[1, 14]

Shell Groups	A	Z_A	B_A	$\partial Z/\partial A$
$Z < 20, N < 20$	30	14.2_5	5.4_7	0.45
	38	17.8_5	4.3_7	
$Z < 20, N > 20$	36	17.1	4.5_8	0.45
	42	19.8	3.9_5	
$Z < 28, N < 28$	40	18.5_5	4.2_0	0.43_5
	54	24.2	3.2_3	
$Z < 28, N > 28$	52	24.1	3.2_4	0.42_4
	63	28.7	2.7_2	
$Z > 28, N < 40$	60	27.1	2.8_8	0.40_2
	74	32.7_5	2.3_8	
$Z < 40, N < 50$	74	32.7_5	2.3_8	0.38_4
	90	38.9	2.0_1	
$Z < 50, N > 50$	86	38.2	2.0_4	0.39_7
	120	51.7	1.5_1	
$Z > 50, N < 82$	120	50.4	1.5_5	0.35_0
	140	57.4	1.3_6	
$Z < 64, N > 82$	136	57.4	1.3_6	0.35_7
	156	64.5	1.2_1	
$Z > 64, N < 106$	156	64.0	1.2_2	0.37
	180	72.8	1.0_7	
$Z < 82, N < 126$	180	73.3_5	1.16*	0.33
	205	81.5		
$Z > 82, N < 126$	200	79.2	1.16*	0.32
	210	82.4		
$Z > 82, N > 126$	210	83.5_5	1.16†	0.35_4
	245	95.9		

* Assumed for consistency with the last section.
† Local solution for B_A.

FIGURE 3 is illustrative of the behavior of Z_A in other shell regions. Present evidence shows Z_A to be linear with A within each of the shell regions. Numerical values of Z_A, B_A, and $\partial Z_A/\partial A$ are given in TABLE 2.

The offsets in binding energy $B_A|\Delta Z_A|$ represented by shifts in Z_A in TABLE 2 are given in TABLE 3.

The data are rather few in the regions where Z or N cross 20 and Z crosses 28, so the offsets are not too certain. No discontinuities in Z_A could be seen at Z or $N = 34$ or at $Z = 40$, although the slope of the $Z_A - A$ curve seems to fall slightly at $N = 40$. The trend of the Z_A data seem to require another small break near $N = 106$ that is not too well understood. The break at $Z = 82$ is offset almost exactly by the close-lying break at $N = 126$, so the absolute values of these opposite breaks in Z_A are therefore in doubt. An analysis of neutron binding by Harvey[15] indicates a break of 2.2 at $N = 50$ and one of 2.2 at $N = 126$; if this latter is true, the $Z = 82$ break should also be larger.

TABLE 3

DISCONTINUITIES $B_A \mid \Delta Z_A \mid$ IN DECAY ENERGIES AT SHELL EDGES[1, 14]

Nucleons	20	28	50	64	82	106	126
Protons	~1.6	~1.1	1.9	~0.6	~0.8	—	—
Neutrons	~0.7	1.0	1.8	—	1.9	~0.5	~1.1

TABLE 4

VALUES FOR δ_A (MEV) AS A FUNCTION OF A

A	40	60	75	100	125	150	175	200	225
δ_A	2.5	2.7	2.8_4	2.8_4	2.4_5	1.8_6	1.6_2	1.5_3	1.47

Taking the B_A values from FIGURE 2, line FF, or TABLE 2, and the Z_A values from TABLE 2, the data for the decay of even-A species may be treated for δ_A by the analog of equation (8):

$$\pm\delta_A = Q^\beta + B_A(Z + 0.5 - Z_A) \qquad (9)$$

where the minus sign applies to even-Z species and the plus sign to odd-Z. The δ_A values show considerable scatter, especially to low values near $N = 50$ and near $Z = 82$, $N = 126$, but not near other shell numbers. This scatter would lead to uncertainty of δ_A values of about 0.3 Mev. The values of δ_A as a function of A are given in TABLE 4. These values, based on experiment, differ considerably from the Fermi estimate $67/A^{3/4}$, which has the values at 40, 125, and 225 of 4.22, 1.79, and 1.15 respectively.

Summary. Quantitative analysis of radioactive decay data shows that β energies have parabolic dependence on Z within a given shell region. The locus of the energy minimum, Z_A, is linear with A, but shows offsets crossing shell edges, given in TABLE 2, and as discontinuities in proton or neutron binding in TABLE 3. A fair representation of

the curvature B_A is given as 78.0 Mev/Z_A except for $A > 180$, where it is 1.16 Mev (FIGURE 2). There is a pairing term ϵ_A accounting for differences in stabilities of odd protons and odd neutrons which occurs just above a few shell edges (TABLE 1). Substitution of these parameters in the equation:

$$Q^\beta = B_A(Z_A - Z - 0.5) + \text{pairing term} \quad (10)$$

permits the prediction of β decay energies Q^β for odd-A species with a precision of about 0.2 Mev from $40 < A < 245$, and explains the absence of stable odd-A isotopes for technetium, cerium, and promethium. The decay of even-A species is also regulated by a more prominent omnipresent pairing term δ_A (TABLE 4) enhancing the decay energy of odd Z members and diminishing the decay of even-Z members. Prediction of the decay of even-A species by equation (9) is good to about 0.5 Mev.

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SECTION OF BIOLOGY

THE FISH IN BIOLOGICAL RESEARCH*

By ROSS F. NIGRELLI†

Plato, writing about aquatic organisms in 400 B.C., stated that "they were made out of the most entirely ignorant and senseless of beings, whom the transformers did not think any longer worthy of pure respiration, because they possessed a soul which was made impure by all sorts of transgression and, instead of allowing them to respire the pure and subtle element of air, they thrust them into water, and gave them a deep and muddy medium of respiration; and, hence, arose the races of fishes and oysters, and other aquatic animals, which have received the lowest habitations as a punishment for their extreme ignorance."[1]

Biologists who have worked with fishes know that they are not so senseless. Many of them show behavior patterns of high order[2] and, when mated, exercise the best in parental care. Their body plan and tissues are essentially the same as in mammals.[21] They have a brain, heart, liver, stomach and all the other vital organs which, histologically and physiologically, differ very little from those in higher animals.[35] Some are vegetarians while others are meat eaters. They all require proteins, carbohydrates and fats for nourishment, and they need the essential vitamins, hormones and minerals for proper growth.[15, 22]

They are also subject to the trials and tribulations not unlike those which affect man. They are susceptible to diseases, many of which are counterparts of human ailments, such as viral and rickettsial diseases, tuberculosis and mycosis, trypanosomiasis and schistosomiasis, tumors and cancers.[20, 23, 26] Fishes kept in aquaria, pools, artificial ponds and hatcheries may develop vitamin deficiency diseases,[33, 34] such as polyneuritis and anemia. They develop degenerative diseases, such as cirrhosis of the liver, and many metabolic disorders including cataracts, gall and urinary stones and diabetes.[20] They also get old and die!

Fishes have always played an important part in the life of the human race. From earliest times, man has made his home near brooks, rivers, lakes, and along the coasts of the oceans. Fishes were their main staple, and among primitive people these animals were often revered as some form of deity. Eventually, man's curiosity led him to seek more information about these aquatic creatures. From the time of Aristotle (384–322 B.C.), Plato's

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† New York Zoological Society.

most famous pupil and dissenter from his school, up to the 16th century, man's knowledge of fishes was meager. Merriman[17] wrote that it was Pierre Belon (1551; "L'histoire des Estranges Poissons Marins") and Guilluame Rondelet (1554; "De piscibus marinis") that broke the 1800-year-old tradition among natural historians of quoting or commenting on Aristotle's knowledge of animals, and began the practice of gathering and reporting first-hand information. Merriman points out further that Belon's history is the first printed book devoted to fishes, and it is called by some the first scientific work in the field of zoology. Rondelet's book contains excellent illustrations and Gudger[11] credits him with the first description and illustration of an abnormal fish (pugheaded carp).

When the transition from the observational or descriptive phase to the experimental phase of science took place in the 18th century, biology developed rapidly. Studies on fishes were used to support, corroborate and illustrate the various theories, principles and laws of biological systems. For example, fishes were used by Abildgaard (1790) to demonstrate the cyclic phenomenon in the development of certain tapeworms (*Ligula* in sticklebacks and birds)[4]; they were used by Darwin (1809–1882) to help support his Theory of Evolution; and by Rouget (1824–1914) to demonstrate the universality of the contractility of blood vessels[6]. In writing on this subject, Rouget stated "I have found the same structure in the capillaries of the epiloon (omentum) of young mammals and in the electric organ of the eel."

It is safe to say that practically every important person in the history of biology and medicine had, at one time or another, used fishes in their studies. It would indeed be difficult to high light all the studies which have contributed most to the advancement of these fields. A few outstanding contributions in the first half of the present century are as follows:

(1) *Experimental Embryology*. The experiments of Stockard[29, 30, 31] which showed the teratological effects (abnormal twining and cyclopia) of temperature, lithium and magnesium in the development of *Fundulus*.

(2) *Genetics*. The contributions of Gordon[8, 10] on the genetics of platyfish and Mexican swordtails, especially the demonstration of Mendelian inheritance of melanomas in these animals.

(3) *Nutrition*. The discovery by McCay and Dilley[16] of Factor H, a growth-promoting vitamin needed by trout, which is present in meat and liver but which is not needed for blood regeneration. These studies led directly to the discovery of folic acid by certain investigators from the Lederle Laboratories.

(4) *Renal Physiology*. The studies of Homer Smith[27, 28] on the anatomy and physiology of fish kidneys from which the theories and principles of renal function in man were developed. Smith[27] wrote "Not only have investigations on the kidneys of fish and the Amphibia contributed enormously to our interpretations of the operations by which human kidney carries out its complex duties, but qualitative and quantitative methods for measuring some of the processes that go on in the normal and diseased human kidney have come almost directly from such studies."

(5) *Endocrinology*. The demonstration by Zondek[36] of the presence of the hormone intermedin in the mammalian *pars intermedia* by the "wedding-dress" reaction in the erlitze (*Phoxinus laevis*), a European minnow.

(6) *Nerve Physiology*. The contributions of Nachmansohn and his collaborators[18, 19] which firmly established the chemical theory of neuromuscular transmission from studies on acetylcholine and cholinesterase in the electric eel. According to Nachmansohn,[18] "To understand the precise function of the enzyme cholinesterase in this phenomenon, its activity had to be connected with events in the living cell, which in the case of nerve, can only be recorded by physical means." For this purpose, the electric eel was used because its powerful electric discharge is identical in nature with the action potential of ordinary nerves. Thus, Nachmansohn, Coates and Cox[19] found that the activity of cholinesterase in the electric organ parallels exactly the action potential.

There are many other major contributions which could be cited but lack of space prevents us from doing so at this time. A survey of the literature (see Zoological Record and Biological Abstracts) for the past 25 years alone will show hundreds of publications dealing with evolution and genetics; anatomy and physiology;[13, 35] experimental morphology;[34] the morphological and chemical aspects of histology and cytology; endocrinology;[13] nutrition;[15, 16, 33, 34] and pharmacology; pathology and parasitology;[20, 22, 26] aggregation and migration phenomena;[2] reproductive and other behavioral studies;[35] and even in aerodynamics! This list does not include the enormous literature

on the commercial aspects of fishery biology. Fishes are also used as assay and test animals for pollution[12] and for such biologics as toxins,[2, 22] hormones,[5, 13] vitamins,[33, 34] antimetabolites[7] and antibiotics (see also recent issues of Progressive Fish-Culturist and Transactions of the American Fisheries Society).

Thus, there has accumulated in the literature considerable basic information on the biology of fishes. Further, our knowledge concerning the management of temperate and tropical freshwater and marine fishes in aquaria,[9] hatcheries, pools, and ponds[14, 25] has improved immensely in the last 10 years. These factors have led to an increase in the demand for fishes for biological research. The following is a list of a relatively few species which have been and can be used for the type of studies indicated above:

(1) *Tropical Freshwater, Viviparous Species.* Guppies (*Lebistes reticulatus*); platies (*Platypoecilus maculatus*); Mexican swordtails (*Xiphorphorus helleri, X. montezumae*); mosquito fish (*Gambusia affinis, Heterandria formosa*); Poecila (*P. vivpara* and *P. nigrofasciata*); mollies (*Molliensia latipinna, M. sphenops, M. velifera*), Limia (*Limia vitatta, L. nigrofasciata, L. tricolor*).

(2) *Tropical Freshwater, Oviparous Species.* Zebra fish (*Brachydanio rerio*); Japanes medaka (*Oryzias latipes*); Siamese fighting fish (*Betta splendens*); paradise fish (*Macropodus opercularis*); dwarf gourami (*Colisa lalia*); hair fin gourami (*Trichogaster trichopterus*); black chinned mouth breeder (*Tilapia macrocephala*); blue acara (*Aequidens latifrons*); Mexican astyanax (*Astyanax mexicanus*); blind cave characin (*Anoptichthys jordani*); electric eel (*Electrophorus electricus*).

(3) *Temperate Freshwater, Oviparous Species.* European and Japanese bitterling (*Rhodeus amarus* and *Acheilognathus intermedium*); carp (*Cyprinus carpio*); goldfish (*Carassius auratus*); common brook and nine-spinned sticklebacks (*Gasterosteus aculeatus, Eucalia inconstans*, and *Pungitius pungitius*); trout and salmon (Salmonidae); sunfishes and basses (Centrarchidae); horned dace (*Semotilus atromaculatus*) and other hardy minnows.

(4) *Temperate Marine, Oviparous Species.* Mummichog (*Fundulus heteroclitus*); broad killifish (*Cyprinodon variegatus*); toadfish (*Opsanus tau*).

(5) *Tropical Marine, Oviparous Species.* Wrasses (Labridae) and parrot fishes (Scaridae).

All of these species are available commercially or can be easily collected. With the exception of the trout, salmon and the tropical marine fishes, many of them can be maintained in laboratory aquaria under proper management[9]. Facilities at universities are often lacking for handling certain fresh-water and marine species. In such cases, it is recommended that the investigator make use of the facilities offered by certain federal, state and private hatcheries, lakeside and marine biological laboratories, and the several public aquaria in this country.

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THE FISH IN ENDOCRINOLOGICAL RESEARCH*

GRACE E. PICKFORD†

In a recent contribution, to which the reader may turn for bibliographic references, Hoar (1951) has discussed the subject of "Hormones in Fish". It is my purpose in the present paper to discuss some practical and theoretical aspects of the problem.

To the medical man, the use of fish in endocrinological research might mean such practical problems as the use of fish in the diagnosis of pregnancy, on which subject there is an extensive but largely discredited literature. Fish have also been suggested as test animals for other hormones. The fish thyroid, for example, is very sensitive to thyrotrophin (Gorbman) and the development of exophthalmos in the killifish has been suggested for the assay of this hormone (Albert). It is also interesting to inquire whether fish hormones can be used to supplement inadequate commercial supplies derived from the slaughter houses. Fish insulin appears to be chemically identical with that derived from mammalian sources (Jensen). In the 1920's, the Canadian investigators (MacCleod, McCormick, and others) made a careful study of fish as a source of insulin but difficulties of collecting the material in fresh condition, and labor costs, appear to have prevented its commercial application. In Japan (Tohyama, *et al.* 1941) and in Germany during the last war (Zeile, *et al.* 1948), it has been found practicable to utilize fish pancreatic islets for the preparation of insulin. Other hormones or hormonal derivatives, of simple chemical composition, such as thyroxin and adrenalin, are probably the same in fish as in higher vertebrates but the protein hormones, which cannot be synthesized, show more or less pronounced phyletic differences. Thus, fish thyroglobulin is different from the mammalian hormone, according to Smith and Matthews, and the gonadotrophins are well known to exhibit marked specificities. Such preparations would be of little or no medicinal value. It seems possible, however, that

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fish ACTH might be utilized, since the active component in mammals is a polypeptide of low molecular weight (Li, 1950). This prosthetic group may prove to be the same in lower as in higher vertebrates.

In another field of research, the artificial induction of spawning with injections or implants of fish pituitary glands has assumed practical importance in pisciculture. In Russia, for example, Gerbilsky and his coworkers have shown that fertilized eggs and viable fry can be obtained in conveniently located hatcheries far from the natural spawning grounds. Species which never mature in captivity, such as the sturgeon, can be induced to produce ripe eggs and sperm. In Brazil, similar procedures are widely used and it has been shown that the glands may be stored in glycerine so as to be readily available when required. It seems probable that the method of pituitary injection will prove useful in the Orient where the practice of fish culture reaches its maximal importance. For example, the species commonly used in the Chinese carp culture ponds do not breed in captivity (Burdon, 1949; Kawamoto, 1950) and the fry must be transported annually from the breeding grounds. In Singapore they are imported from China via Hong Kong, a journey of a week, in large open tubs aerated by hand operated paddles. Similarly, in Thailand, a favorite food is the giant catfish, *Pangasius*, which is reared and fattened in the culture ponds but which cannot be bred in captivity.

In fish as in higher vertebrates, there is a growing body of literature concerned with the role of hormones in the regulation of behavior patterns. This field of research owes much of its early impetus to the pioneer work of Noble, so abruptly terminated by his early death. It is difficult to study problems of fish endocrinology without becoming involved in behavior problems. Such an experience occurred recently at the Bingham Oceanographic Laboratory, during the course of routine tests on pollack pituitary fractions (Pickford, 1952). We discovered that injections of fish pituitary gonadotrophin induced characteristic S-shaped spawning spasms in hypophysectomized killifish. Since the gonads of such fish are in total regression and since the response develops rapidly, in 15 to 20 minutes after the injection, it seems probable that we are dealing with a direct stimulation of the nervous centers. This situation is contrary to that in higher vertebrates, in which sexual behavior is mediated by the sex hormones, and only indirectly by the gonadotrophins (Beach, 1948). The same response can be elicited from normal fish of either sex at any time of year, but emission of the sex products was only observed when the recipient was close to natural spawning. Our preparation was apparently free from the follicle stimulating factor since continued injections over a prolonged period of time failed to induce growth of the gonads. Experiments with mammalian preparations revealed that the luteinizing hormone will elicit the spawning reflex, but that FSH and prolactin are inactive. Prolonged treatment with mammalian FSH, on the other hand, stimulates the growth of the testes in hypophysectomized fish. In one of Noble's experiments, it was shown that brooding behavior in the jewel fish could be induced with various pituitary preparations provided the fish had had previous spawning experience. Therefore, we made some experiments with young fish taken in early spring before their first breeding season. Injections elicited a typical response which is thus independent of previous spawning experience.

A great deal of research, reviewed by Hoar has been directed towards the little understood function of the fish thyroid. Passing over these problems and neglecting the field of embryology, we may turn to theoretical considerations of comparative anatomy and physiology. At the turn of the century, the lower vertebrates were extensively studied with a view to learning more about the origin and evolutionary significance of the vertebrate endocrine system. Broadly speaking, it became evident that the same pattern prevails throughout the craniates. With some exceptions, all possess the same endocrine glands and elaborate similar hormones. Little is known about endocrine functions in the prochordates. The endostyle of urochordates and cephalochordates does not accumulate radioactive iodine (Gorbman). The subneural gland of urochordates is generally regarded as a pituitary homologue and there is evidence that it functions as such. The literature on this subject is reviewed by Carlisle (1951). Chromaffin tissue occurs in the nervous system of many invertebrates but, in general, the endocrine system of the vertebrates must be rated as one of the distinctive features of the phylum on a plane with the morphological characters commonly used in text book definitions. One

might define the vertebrates as a phylum in which hormonal regulation plays a major role in mediating the adjustments of the animal to its environment. Thus, throughout the craniates, blood sugar is regulated by the internal secretion of the pancreatic islets; shock reactions are mediated by the adrenal; the maturation of the gonads is mediated by the pituitary; and so on. We are not yet sure that the basal metabolism of fish is regulated by the thyroid hormone, but recent work points in this direction.

The physiological evolution of hormonal function within the phylum presents many interesting problems. There is, for example, the question of changing target organs. Prolactin is known to be present in the pituitary of all chordates, with the possible exception of fish. In amphibia, this hormone participates in the regulation of the reproductive cycle, inducing oviducal secretion in frogs and toads (Houssay, 1952) and initiating the spring migration of newts to the ponds (Chadwick, 1941). Conversely, in lower vertebrates, the role of intermedin in chromatophore regulation is well understood but its function in higher vertebrates is obscure. There are important gaps in our knowledge of fish endocrinology. A parathyroid gland, for example, is said to be absent in fish. This assumption would seem to be *a priori* improbable in the case of the bony fishes, but no one appears to have studied the effects of parahormone on calcium and phosphorus metabolism in this group. Teleost fishes possess an endocrine tissue, the corpuscles of Stannius, which is without counterpart in higher vertebrates. These glands are said to be unnecessary for life (Vincent, 1898) and recent work in our laboratory has shown that they are independent of pituitary control.

In conclusion, I should like to give a brief review of some of the recent investigations which have been in progress at the Bingham Oceanographic Laboratory.* We have made a careful study of the hypophysectomized male killifish with a view to its use for the detection and, ultimately, it is hoped, for the assay of fish pituitary hormones. The hypophysectomized killifish does not grow, although renewed growth may be induced with purified mammalian growth hormone. In confirmation of previous work (Matthews, Burger), the gonads are in regression and the thyroid is inactive, but the adrenal cortical tissue does not show the expected state of atrophy even after a period of 6 months. Hypophysectomized fish nearly always develop carbonate-apatite kidney stones and we discovered, to our surprise, that hypophysectomized killifish cannot survive in fresh or diluted sea water. In collaboration with Dr. A. E. Wilhelmi of Emory University, we have been studying purified fish pituitary fractions. For this purpose, we collected 325 gm. of fresh frozen glands from pollack and other fish, representing an estimated 17,000 heads. From this material Dr. Wilhelmi prepared 12 different fractions which were returned to us for study. Among these, three closely associated fractions contained the spawning reflex hormone. Further purification of the pooled samples has yielded a highly active preparation that will elicit the response at a dosage level of 10 μg per gram weight. The fish growth hormone fraction has been subjected to a preliminary investigation. This preparation has the physical and chemical properties of purified beef growth hormone, but Wilhelmi found that, when injected into rats, it induced a small growth response in the first four days, followed by progressive weight loss. When injected into hypophysectomized fish, it induces a weight increase and resumption of growth in length. We have compared the response with that elicited by purified beef growth hormone at the same dosage level, 10 μg per gram weight thrice weekly. The final increment at the end of several weeks of treatment, is of the same order with fish as with beef growth hormone. The ultimate effect would thus appear to be independent of the source of the hormone.

* Supported by a grant from the National Science Foundation.

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POPULATION STUDIES OF THE ROSEFISH*

By ALFRED PERLMUTTER†

Our first thought in studying a population of fish is to set up experiments in aquaria. In the laboratory, it is possible to exercise complete control over both the environment and the population, and to determine theoretical aspects of population dynamics. Yet, no matter how complete our laboratory findings, it is still necessary for us to go into the field to test the theories evolved. Because of this, most recent population studies of fish are carried on directly in nature, in the streams, lakes, or oceans. Here, however, the biologist exerts little control over the environment and the population. Predominately, population studies are of fish of economic importance, since the studies are usually complex and costly and only such applied research receives financial support. The approach of a fishery biologist to the study of a fish population of economic importance may be illustrated by a brief summary of the study of the rose fish, *Sebastes marinus* (Linnaeus), one of our more important food fishes.

The rosefish is a common inhabitant of the North Atlantic Ocean. It is abundant off northern Europe as far north as Bear Island in the Arctic Ocean and large quantities are taken off Iceland, Greenland, and Newfoundland, as well as in our own offshore waters north of Cape Cod. In American waters, it is most commonly found in depths of from 60 to 1?0 fathoms. Previous to 1935, only a few thousand pounds were taken. Largely through technological developments, such as quick-freezing and attractive packaging, consumer demand for the rosefish steadily increased, so that by 1946, the annual catch rose to 180 million pounds (FIGURE 1).

Despite the increase in the total catch, the fishermen reported that fish were becoming scarce in the adjacent New England grounds; i.e. the Gulf of Maine grounds. During the period studied, 1942 to 1946, the rosefish fishery was active, not only on the adjacent Gulf of Maine grounds, but also on the more distant, western Nova Scotia banks (FIGURE 2). The records of total catch, therefore, were broken down into two categories: (1) The catch from the Gulf of Maine grounds; and (2) the catch from western Nova Scotia grounds. It is, at once, apparent from the examination of FIGURE 2 that the catch from the Gulf of Maine grounds had been decreasing

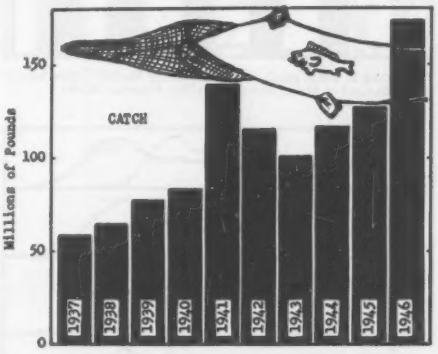

FIGURE 1. Total catch of rosefish of the United States fishery in western Atlantic waters.

from the year 1942 to 1946. In 1942, it was over 110 million pounds, while by 1946, it was less than 80 million pounds. On the other hand, the catch from the Nova Scotia banks had risen sharply from 1942 to 1946, from about 5 million pounds to over 70 million pounds. Since running time to and from the more distant Nova Scotian banks is greater than to the adjacent Gulf of Maine grounds, it is to be expected that if fish were abundant in the Gulf of Maine, the boats would not go to the western Nova Scotia banks to make their catch. Something then had happened to the abundance of fish in the Gulf of Maine. This is reflected in the changes in annual average size composition

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† New York State Conservation Department. Data collected while a member of the U. S. Fish and Wildlife Service.

of the catch of rosefish taken by Gloucester draggers in the Gulf of Maine (FIGURE 3).

In the rosefish, the females grow larger than the males. The sexes have been plotted separately. Note that, in 1942, both the male and female length frequency curves are unimodal in

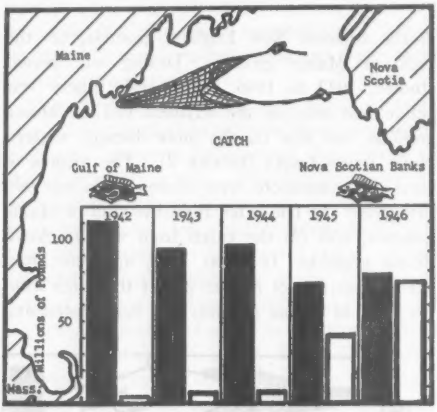

FIGURE 2. Total catch of rosefish of the United States fishery from the Gulf of Maine and western Nova Scotian Banks.

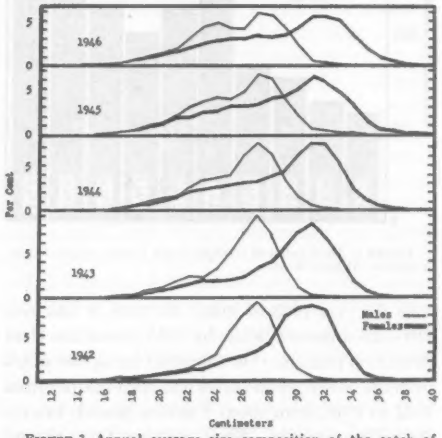

FIGURE 3. Annual average size composition of the catch of rosefish taken by Gloucester draggers in the Gulf of Maine.

character. During the following four years, there is progressive development of a secondary mode at a somewhat smaller size which is especially marked in the length frequency curve for the males. If nothing else were known, this bimodality could be explained in several ways:

(1) It is the result of an influx of smaller fish, possibly from nursery areas.
(2) It is the result of the migration of larger fish out of the area.
(3) The larger fish are being caught more rapidly than they can be replaced.

Length at maturity studies were now carried on to determine at what sizes the rosefish matures. It was found that over 90 per cent of the males, 25 centimeters in length, and of the females, 28 centimeters in length, were mature. Fish over this size were, therefore, considered mature (FIGURE 4).

From information obtained on each fishing trip by daily interviews with fishing captains, together with other statistical data gathered from the industry, a catch per rosefish day was computed as an estimate of relative abundance. In doing

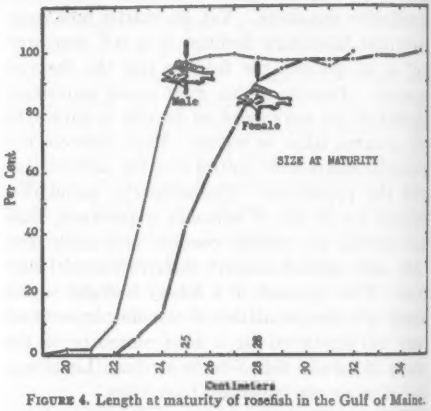

FIGURE 4. Length at maturity of rosefish in the Gulf of Maine.

this, the catch per day of males less than 25 centimeters and of females less than 28 centimeters (including both mature and immature fish) was designated "recruits"; while the catch per day for males and females above these sizes (mostly mature fish) was designated "matures" (FIGURE 5).

As can be seen, the catch per day of the "recruits" has remained steady from 1942 to 1946, ranging from a little over 2,500 pounds per day to about 3,000 pounds per day, while the catch per day of "matures" has dropped from 14,000 pounds per day to 8,500 pounds per day. It appears, then, that the reason for the bimodality of the length frequency curves of rosefish in the Gulf of Maine is not the influx of small fish, but may be due to the fact that the larger fish are moving to other grounds, or that they are being taken out faster than they can be replaced.

Our next step, then, was to determine whether the larger rosefish in the Gulf of Maine were mov-

ing out of the area. Because the rosefish is caught at such great depth, it does not reach the surface in a condition suitable for tagging. Its eyes are popped, the intestines protrude from the mouth, and the skin is flabby due to the sudden change in pressure as the fish is rapidly hauled up in the otter trawl. It was found, however, that the copepod parasite, *Sphyrion lumpi* (Krøyer), was practically specific for the rosefish in the American Atlantic areas. In the Gulf of Maine grounds,

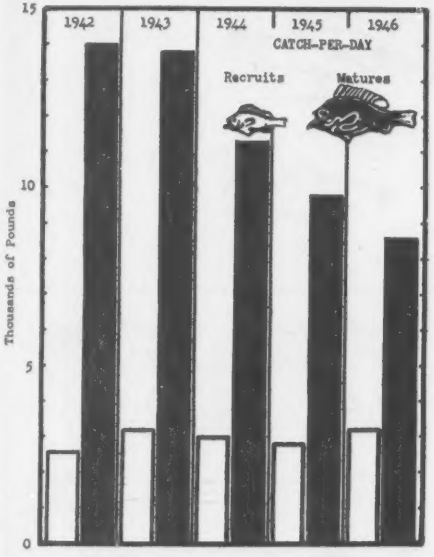

FIGURE 5. The annual average catch per day of "recruits" (males less than 25 cm., females less than 28 cm.), and "matures" (males 25 cm. and longer, females 28 cm. and longer) by a sample fleet of Gloucester rosefish draggers.

Sphyrion lumpi is extremely abundant. Infection of the catch may range from less than 1 per cent to over 25 per cent, depending on the season and area taken. On Nova Scotian grounds, although thousands of fish were examined, not a single specimen of *Sphyrion lumpi* was ever found. The larger fish, therefore, could not be moving out of the Gulf of Maine, since, if this were true, they should appear on the neighboring Nova Scotian banks, and fish infected with the copepod parasite, *Sphyrion lumpi*, would be present there. We could only conclude that there is no migration of fish from the Gulf of Maine grounds to the Nova Scotian banks. Consequently, the decrease in abundance in the Gulf of Maine grounds could not be due to movement of fish from this area.

Our final step was to determine whether fish were being caught faster than they could be replaced. Age and growth of the rosefish, as shown on their scales, indicated extremely slow growth. The average growth was less than 1 inch per year to about the ninth year, at which time the fish were mature, (FIGURE 6). Mature fish were not studied, but it can be anticipated that the growth rate would be even less after maturity.

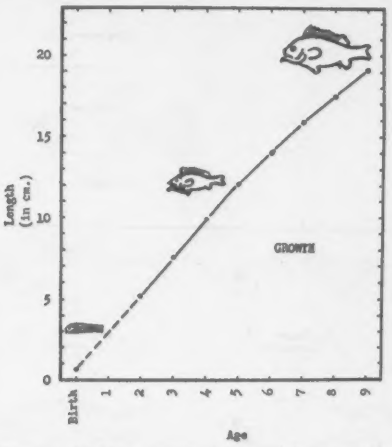

FIGURE 6. Calculated growth of the rosefish in the Gulf of Maine to the ninth year.

The slow rate of growth would explain the drop in the catch per day of rosefish in the Gulf of Maine. In any virgin fishery, particularly where the fish are slow growing, it can be expected that a relatively few of the larger, heavier, and older fish, which have been accumulating over the centuries, will at first contribute heavily to the catch, resulting in a high catch per day. As the population is more heavily fished, these are reduced in number, and the smaller, lighter, and younger fish become more predominant in the catch, and the catch per day declines. It necessarily follows that the catch per day, in subsequent years, will be much lower than that attained at the beginning of the fishery.

THE USE OF FISHES IN THE EVALUATION OF HEREDITY IN ATYPICAL PIGMENT CELL GROWTH*†

By MYRON GORDON‡

In evaluating the influence of hereditary factors in the development of one of the spontaneous cancers, the melanoma, the platyfishes, and swordtails are the most valuable experimental animals among the vertebrates. This is so because we know something of the inheritance of their basic black pigment cells. Some of these cells, or melanophores, have been shown to initiate the development of melanomas in fishes that are genetically imbalanced.

The inheritance of two kinds of melanophores, the smaller (micromelanophores) and the larger (macromelanophores) in the common platyfish of Mexico and Central America, may be referred to two dominant genes; one autosomal, the other sex-linked. The autosomal inheritance of smaller melanophores is illustrated by FIGURE 1 and the sex-linked inheritance of the larger ones by FIGURE 2.

In studying the results of inheritance of the large and small pigment cells, it was noted that, while there is some variation in the pigmentary patterns among the members of the brood, no abnormality of pigment cell growth appears in any of them. This may be attributed to the circumstance that the individuals involved in these matings are members of the same species and of the same stock.

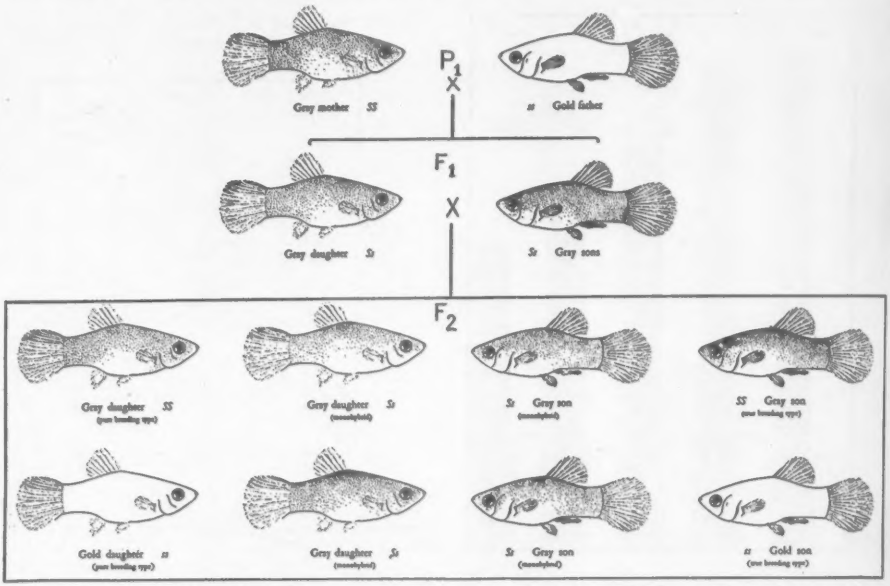

FIGURE 1. A platyfish that carries micromelanophores appears gray. One without these small pigment cells is of golden color. When a gray platyfish (*SS*) is mated with a golden (*ss*), all the members of the first generation are gray (*Ss*).
When two gray first generation platyfish are mated (*Ss* x *Ss*), there are three gray platyfish to one golden in the second generation. This is, in part, evidence that the gene for the small black pigment cells is a simple Mendelian dominant.

In an experiment illustrated by FIGURE 3, two important results were discovered: first, when a spotted platyfish (*Xiphorphorus maculatus*) that carries dominant genes for both macromelanophores and micromelanophores is mated to a distinct but closely related species, the swordtail (*Xiphophorus helleri*), their hybrids develop spontaneous melanomas somewhere on the body; second, when a platyfish carries only the micromelanophore gene or is a recessive for both types of pigment cell genes, their hybrids with the swordtail are normal with respect to the develop-

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‡ Genetics Laboratory of the Aquarium, New York Zoological Society at the American Museum of Natural History, New York.

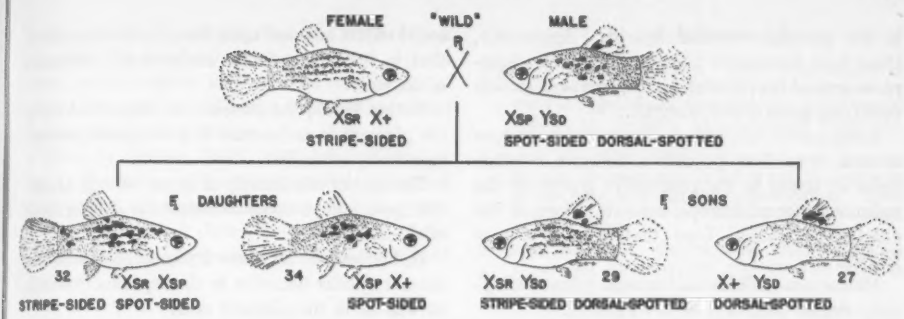

FIGURE 2. In this mating, a stripe-sided female (macromelanophores are arranged in stripes across the body) is mated with a spotted-dorsal and spotted-side male platyfish (macromelanophores are in the dorsal fin and on the sides of the body). Note (1) that the spotted-dorsal trait is transmitted from the father only to the sons; (2) that the spot-sided trait is transmitted from the father only to his daughters; (3) that the stripe-sided pattern is transmitted from the mother to one half of her sons and daughters. This type of inheritance may best be explained on the basis of sex-linkage. The type of sex-linkage displayed here is of the XX female—XY male, somewhat similar to that found in man.

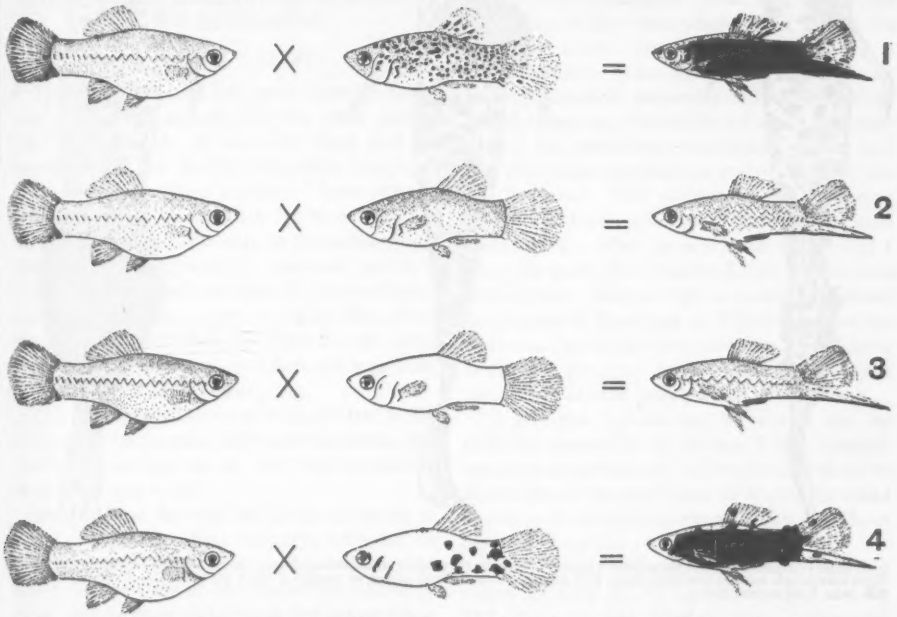

FIGURE 3. In the first mating between the spotted platy and the swordtail, the micromelanophore and macromelanophore genes are contributed by the platyfish parent. The hybrid develops melanoma.
In the second mating, the micromelanophore gene of the platyfish is involved. The hybrid is normal with respect to its pigment cell growth.
In the third mating, the golden platyfish is recessive for both types of black pigment cells. The hybrid is normal.
In the fourth mating, the macromelanophore gene in the platyfish is involved. The hybrid develops melanomas.
Other types of matings, not shown in these figures, indicate that, even though an albino swordtail is used in a similar mating, their hybrids that carry the large black pigment cell gene will develop melanomas.

ment of the black cells. On the other hand, a platyfish carrying the dominant sex-linked gene for macromelanophores alone, mated with a swordtail, produces hybrids that develop melanomas (FIGURE 4).

The conclusion was reached that the large black pigment cells, rather than the smaller ones, were responsible for the initiation of the spontaneous growth of melanomas in the hybrids. Carrying the analysis of these experiments further, it may be said that the atypical growth of macromelanophores may be attributed to the genic imbalance

in the platyfish-swordtail hybrids. Apparently, there is an interaction between the macromelanophore gene of the platyfish and pigment-cell growth modifying genes in the swordtail.

Using genetic methods to obtain melanomatous animals, it has been possible to obtain a complete series of stages in the progressive growth of the melanomas for microscopic analysis. Some of the conclusions reached from these studies are as follows:

Melanomas in fishes and in man follow biologically similar pathways of development.

ential effects imposed upon them by their position; that is, by the particular environment influences of the body.

Within limits, the presence or absence of melanin pigment in melanomas is a reversible process, genetically controlled.

The spatial relationship of genes as well as specific gene combinations influence the development of specific tumors.

Hybridization, in many instances, leads to abnormal cellular behavior in the reproductive cells as well as in the pigment cells.

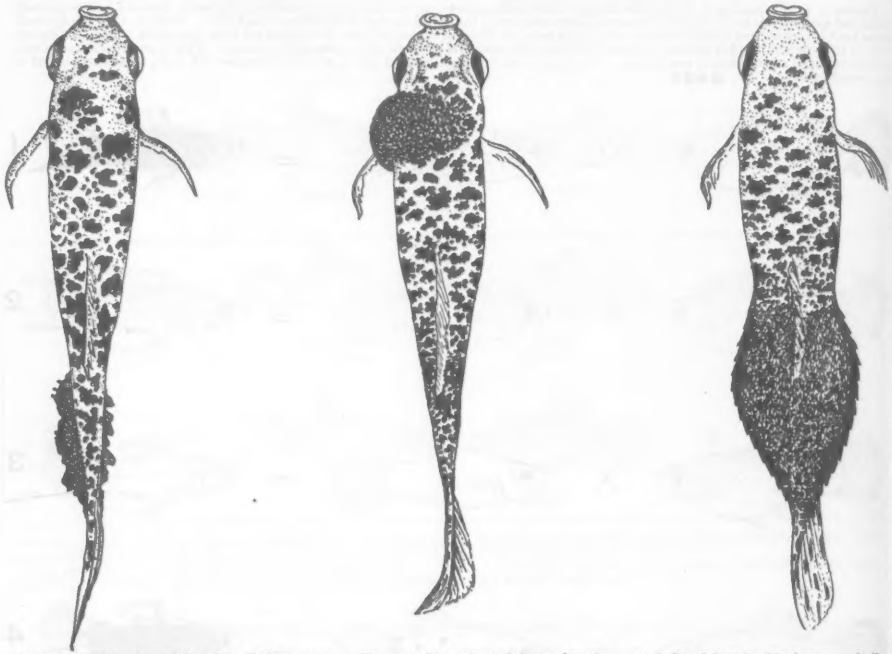

FIGURE 4. These three fishes show distinct tumors. They are the product of the mating of a spotted platyfish and a Mexican swordtail. Upon microscopic examination, these fishes show advanced stages of melanomas, or cancers of black pigment cells. Drawings represent fish twice their normal size.

The melanocyte is the common cell type in melanomas of fish, mouse, and man. This has been revealed when tissue cultures of comparable material has been studied.

Melanotic tumors in fishes are transplantable homotypically and in siblings.

The site of melanoma development can be controlled genetically.

The difference in the structures of the melanomas may be attributed, in some measure, to the differ-

Fundamentally there is no difference in the reaction between the intraspecific hybrid members of two geographical populations and the interspecific hybrids with reference to their atypical macromelanophore growth.

The results of all the genetic experiments concerned with normal and atypical pigment cell growth may be explained within the framework of present-day principles of Mendelian inheritance.

The hereditary control of melanomas in hybrid

fishes rests not on one gene but on a constellation of genes. To be effective this assemblage of genes must contain within it a gene for macromelanophores, the pigment cells that are sensitive to the influence of genic imbalance.

Recently Gordon (1948, 1951) has reviewed at length the subject of hereditary control of normal and atypical pigment cell growth, and Berg and Gordon (1953) have shown the relationship of the gonads to the development of melanomas in hybrid fishes.

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SECTION OF PSYCHOLOGY

STIMULUS DISCRIMINATION AND MORSE CODE LEARNING*

By FRED S. KELLER†

The January issue of this year's *Scientific American* contains an excerpt from the same journal for January, 1853. It is to the effect that the operators of the Buffalo-Milwaukee telegraph, "working under Morse's patent," have stopped using the visual signals made by Morse's instrument and pay attention only to the *auditory* cues that the signals provide as they are recorded. "The different sounds are made by the striking of the pen lever upon a piece of brass: thus, three raps in rapid succession are made for the letter 'A,' two raps, an interval, and then two raps more are made for 'B,' and so forth."

This item nearly led me to write a letter to the editor, for two reasons: These operators were not the first to copy code by ear, they were apparently using the wrong code!

Samuel Morse designed his famous telegraph to record *visual*, rather than auditory, code, but he probably recognized, as early as 1835 or 1836, that each code signal had its own distinctive pattern of sound, and he made this clear in the patent specifications drawn up in 1837–38.[9] Moreover, he had himself seen his recorder used as a "sounder" at least six years prior to 1853. He describes his experience in detail:

"The time of the incident was soon after the line was extended from Philadelphia to Washington, having a way station at Wilmington, Delaware. The Washington office was in the old post-office, in the room above it. I was in the operating room. The instruments were for a moment silent. I was standing at some distance near the fire-place conversing with Mr. Washington, the operator, who was by my side. Presently one of the instruments commenced writing and Mr. Washington listened and smiled. I asked him why he smiled. 'Oh!' said he, 'That is Zantzinger of the Philadelphia office, but he is operating from Wilmington.' 'How do you know that?' 'Oh! I know his touch, but I must ask him why he is in Wilmington.' He then went to the instrument and telegraphed to Zantzinger at Wilmington, and the reply was that he had been sent from Philadelphia to regulate the relay magnet for the Wilmington operator, who was inexperienced in operating...

"I give this instance not because it was the *first*, but because it is the one I had specially treasured in my memory and frequently related as illustrative of the practicality of reading by *sound* as well as by the written record. This must have occurred about the year 1846." [9]

As for the second point, the *Scientific American* names the signal for "A" as "three raps," and for "B", "two raps, an interval, and ... two raps more." Yet the code to which these signals belonged was presumably out of date by 1853.

The first Morse code, invented by Morse in 1832, was composed of ten signals. These signals represented the ten digits. Morse pictured them as dots and spaces between dots. Thus, the numbers 1, 2, 3, 4, and 5 were represented by one, two, three, four, and five dots, respectively, with each sequence followed by a pause that was perceptibly

* This paper, illustrated with lantern slides, was presented at a meeting of the Section on March 16, 1953.

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greater than the intra-signal space between dots. Six, 7, 8, 9, and 0 were also indicated by one to five dots, but the pause after each string was two-thirds again as large as that which followed each of the first five digit signals.

Originally, Morse had intended to represent 6, 7, 8, 9, and 0 by six, seven, eight, nine, and ten dots. He tells us, however, that "a few minutes'

Character	Morse's Code No 2[1]	Morse's Code No. 3 (American Morse)	International Morse
A	·–	·–	·–
B	·· ··	–···	–···
C	· ··	·· ·	–·–·
D	··· ·	–··	–··
E	·	·	·
F	· ···	··–	··–·
G	·· ·	– –·	– –·
H	····	····	····
I	·–	··	··
J	·· ·	·––·	·– – –
K	–·–	–·–	–·–
L	—	—	·–··
M	–·	– –	– –
N	–·	–·	–·
O	··	· ·	– – –
P	·····	·····	·––·
Q	··–·	··–·	– –·–
R	· ·	· ··	·–·
S	·–·	···	···
T	– –·	–	–
U	·– –	··–	··–
V	–	···–	···–
W	·––	·– –	·––
X	– –	–···	–··–
Y	·–	·· ··	–·– –
Z	·–·	··· ·	– –··
1		·– –·	· – – – –
2		··–··	·· – – –
3		···–·	···· – –
4		····–	····· –
5	?	– –	·····
6		·····	–····
7		– –··	– –···
8		–····	– – –··
9		–··–	– – – – ·
0		— —	– – – – –

FIGURE 1. Three Morse Codes.

reflection showed that after *five* dots or points the number of dots became inconveniently numerous in indicating the larger digits."[11] This interesting 'reflection' probably stemmed from Morse's failure to judge, correctly, at a single glance, the larger number of dots. This you can easily see for yourself:

....

.....

Psychologists know that Morse's failure was not without precedent. Charles Bonnet, the Swiss naturalist and philosopher, had argued, back in 1760, that the mind could have no clear impression of more than a very limited number of objects (he said *six*) at one time. Psychologists may also note that Morse anticipated the observations of Sir William Hamilton, who threw marbles on the floor and found it "difficult to view at once more than six, or seven at most, without confusion." They remember, too, that Jevons, the logician, tossed beans into a little round box and found "absolute freedom from error in the numbers 3 and 4", but failed to judge the number 5 correctly in five per cent of the cases. It is clear to all of us today that Morse was making contact with the "span of attention" problem.[20]

In a very modern setting, Morse's observation has been paralleled almost exactly in part of a study by Saltzman and Garner[12] at Johns Hopkins about five years ago. These investigators showed subjects from one to ten visual dots, in a straight line, and asked them to judge the number at each showing. They found that, with increasing dot number, there was a decrease in the accuracy of the reports. Moreover, the time required to report increased as the number of dots increased, even for numbers below the mystic five or six. Morse's "reflection" seems quite up to date!

The first Morse code was cryptographic. There were numbers for all of the letters and many of the words of the English language. Morse spent many hours in building a "telegraphic dictionary" to be used in coding and de-coding messages. These hours were wasted. His dictionary was barely completed when he decided to use an "alphabetic" code, in which each letter had its own signal. This second Morse code is shown in FIGURE 1.

It was probably introduced in 1838, and it is the code to which the *Scientific American* referred in its 1853 item. It was composed of the now conventional dots and dashes, and occasionally employed a special intra-signal space. This space can be seen in the signals for *B*, *C*, *D*, *F*, *G*, and *R*. You will note, too, that the signals for *G*, *I*, and *S* also did service for *J*, *Y*, and *Z*. Morse was a frugal man, or afraid that too many signals would reduce the appeal of his code!

But Code No. 2 had a short life. Within four years, Morse arrived at his third and final offering. This code followed upon a trip to a printing office where Morse determined the amount of type on hand for each letter in the compositor's case. This

was done for the express purpose of relating the 'size' of the signal to the frequency of its usage.

Code No. 3 was employed in transmitting the famous message (*What hath God wrought!*) from Washington to Baltimore and back again on May 24th, 1844. It is the code that we now call "American Morse." It is also the code that should have been well known to the telegraph operators on the Buffalo-Milwaukee wire nine years later! It is here shown in FIGURE 1. This is the code that you may still hear occasionally in country railroad stations or on the broadcasts of baseball games.

Morse, in making up his first code, apparently recognized an important discriminative problem when he noted that visual dots became "inconveniently numerous" when they exceeded five. We have also given him credit for having anticipated the use of auditory rather than visual signals in transmitting the code. It does *not* appear, however, that he was ever aware of some of the discriminative problems raised for those whose task it would be, in later years, to receive the code *by ear*. His third code, although quite well suited for the work ahead, was nevertheless defective in one or two respects.

The first and least important fault had to do with those dot signals that contained an extra internal space. That is, the signals for *C*, *O*, *R*, *V*, and *Z* in FIGURE 1. Careful spacing of these signals, and of their component dots, was required, if certain words were to be copied without error. For example:

P I E R C E

. . . .

This difficulty, which came in with the hand-sending of the signals, was seldom very great, however, and today is virtually non-existent. *International* Morse code, which replaced these signals by longer ones, composed of dots, dashes, and small spaces only, is now almost universally employed in radiotelegraphy.

The second defect in the third code, American Morse, was rooted mainly in five signals: *6*, P, *H*, *4*, and *8* (see FIGURE 1). The fundamental difficulty with all of them is the same as that recognized by Morse when he ruled out sequences of more than five dots in his first code. They are sources of sometimes ineradicable confusion. For example, *6*, unless it occurs in a context of numbers, is commonly mistaken for *P*. *P*, when alone or in cipher, may often be called *H*; *H* may be called *S*; *4* may be called *V*; and *8* may be called *B*.

Down through the years, telegraphers became increasingly aware of this difficulty, but they seldom complained. There was little notion of either the prevalence of such confusions or of the direction that they most commonly took (*6* may be called *P*, but *P* is less likely to be called *6*, etc.). Some operators, having a good ear or a very quick wit, seemed to have no trouble. Others, less gifted, were often plagued by their failures to discriminate. With the advent of the semi-automatic key or "bug", early in this century, even the experts got into trouble once in awhile. The bug could be adjusted to provide very high rates of dotting. It was not only hard for the receiver to copy these dot signals, it was hard for the sender to transmit them accurately. Most *receivers* met the problem by relying upon context. The word *Please* does not begin with an *H*; *both* is not spelled b-o-t-s; and *March 1P* is not a date on any calendar. *Senders* met their problem in different ways. Sometimes they just "turned on *P* and let it run" for 10 dots or more. At other times, they shifted from bug- to hand-sending at critical points, and so on. All this took place day after day, year after year, in every busy railroad or commercial telegraph office of our country. Telegraphy became, on occasion, a high-tension performance, comparable to that provided by Pavlov when he pushed his dogs to the limit of their discriminative powers; but there was scarcely a murmur of protest from those most deeply involved.

Things might have been different if the telegraphers, or their employers, had read the psychological literature of the day. For example, they might have found in the British journal, *Mind*, for 1886, an interesting report from the Psychophysical Laboratory of Johns Hopkins University.[3] The writers of the report were two young men who were to become well-known in American psychology. Their names were G. Stanley Hall and Joseph Jastrow. They had conducted an experiment in which their subjects were asked to count the number of clicks made by a quill toothpick as it passed over cogs on the perimeter of a revolving metal plate. The number of clicks ranged from 2, at the bottom of the scale, up to as many as 65, at the top. The subjects made anywhere from three to ten judgments for each click number and at several rates of clicking.

Hall and Jastrow permitted each subject in this experiment to listen to each click sequence as many times as he wished, until he felt that his

estimate of click number could not be improved. He was free to use every device of counting or grouping that he could think of in reaching an accurate estimate. But, in spite of all this, *underestimation of click number was clearly present in every instance.* Practice reduced the error considerably but did not eliminate it. Hall and Jastrow point out that the addition of a single click, even to as small a group as three, demands that the interval between clicks be increased appreciably if the larger number is to be reported correctly. Clearly, the poor telegrapher, often compelled to cope with just as fast a rate of clicking, but without benefit of more than an occasional immediate repetition of click number, would have felt underprivileged after reading such an account; and this was before the bug had been invented!

The Hall–Jastrow study was inspired by some observations at Hopkins on the reading and counting of visual trains of letters. These observations were made by James McKeen Cattell, fresh from Leipzig, where Wundt had become interested in the rhythms imposed by subjects as they listened to various rates of uniform beats. One of Wundt's pupils, Georg Dietze, had published on this topic a year in advance of the Hall–Jastrow paper (which was itself entitled *Studies of Rhythm*). In 1894, after Hall had moved to Clark, Thaddeus Bolton, one of his pupils, came out with a study much like Dietze's. This was followed, more or less directly, by the rhythm studies of Meumann, Koffka, Stetson, and, especially, Woodrow. Curiosity about mere error in judging auditory number was easily stifled by this interest in more dramatic phenomena. More than sixty years were to pass before any psychologist turned into the path suggested by the Hopkins study.

Revival of interest in this problem came at the outset of World War II. The setting was a very practical one. Good radio operators were needed for war work at a rate faster than they could be turned out by the service schools. There was particular interest in reducing the time required for teaching men and women to receive International Morse code.

This code, earlier known in this country as *Continental*, because of its origin, was a variation of American Morse that had been adopted for our military use prior to World War I. It differed from Morse's code in two major respects, as may be noted in FIGURE 1. It did away with the larger intra-signal spaces, as in *C*, *O*, *R*, *Y*, and *Z*, and it also offered an orderly arrangement of signals for the digits from *1* to *0*. As for the old dot problem of American Morse, you will note that the worst offender, the signal for *6*, is gone. Yet, a glance at the signals for *5*, *4*, and *6* of the new code may suggest that the problem had not yet been completely solved.

There was, however, no evidence from the training centers to support such an expectation; nor was there any from the body of code-learning data that had been collected since World War I. As late as 1943, in Taylor's[18] review of the literature in the field, there was no more than the barest of recognitions that some signals were harder to deal with than others.

The first classroom research on the difficulty of the signals in International Morse code came as the outgrowth of a new method—the "code-voice" method—of teaching the code.[6] This method was developed at Columbia University during the period from 1941 to 1943. It was a form of the paired-associates procedure and consisted of three basic steps: (1) sounding a code signal in the ear of a student; (2) giving him three or four seconds in which to write down a letter or digit; and (3) telling him the correct name of the signal. The student printed his letters and digits (and the corrections when required) on a special practice sheet. A sample form of this sheet is shown in FIGURE 2, filled in from an actual record.

An entry within the upper square of any block of ten like those shown in the figure represents the student's response to the signal *before* it was identified. No entry means no response. An entry in the lower square of any block is made only when the response to the signal has been incorrect or did not occur. Thus, in response to the first signal, the student in this case wrote *0* when he should have written *S*. In response to the second signal, he wrote *A*, correctly; and he failed to respond to the third signal at all before his instructor said "Two;" and so on, throughout the 100-signal run, in which this student made 83 errors of omission or substitution.

This method can provide something more than a running account of a student's progress in terms of per cent correct. It can also tell him, after a bit, exactly where his trouble lies in learning—which signals are hard and which are easy, and which ones are mistaken for which others. Moreover, it gives his instructor the same information, making it possible for him to measure the relative difficulty of signals for the entire class. It may not surprise you to hear that two studies of signal

difficulty were carried out before the first account of the code-voice method itself had been published.

In one of these studies, Spragg[15] examined the responses of 19 students in a code class at Queens College. The signals were machine-sent and for the alphabet characters only. In the other study, at Columbia University, Keller and Taubman[7] used 50 subjects, handsending, and all 36 signals. Both studies took their subjects well above the point of mere mastery of the code signals.

In TABLE 1 are shown the rank orders of difficulty provided by these two studies, together with one from a slightly later investigation by Plotkin.[10] Plotkin's study used 20 subjects, hand-sending, and all 36 signals. The correlations between these rankings, based on alphabet errors of substitution only, are high: +.91 between the Spragg and Keller-Taubman ranks, and +.82 between the Plotkin and Keller-Taubman ranks.

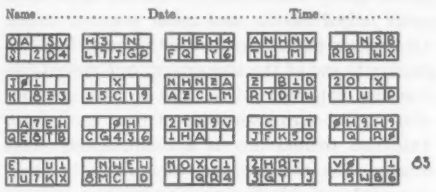

FIGURE 2. Sample code-voice practice sheet.

These rank orders possess one puzzling feature. In view of my remarks about the defects of American Morse and the errors in judging auditory number, the rankings reflect very little trouble with signals containing strings of dots. Why, especially, is the signal for *H* (four dots) so easy to learn? It is 17th in Spragg's list, 16th in the Keller-Taubman list, and 12th in Plotkin's.*

With respect to this question, several points may be made. First, only the alphabet confusions are considered in these rank orders, since Spragg did not use the digit signals. Hence, the highest number of dots in any signal was *four*, and we would look for less difficulty with this number in the absence of a higher one (five) for which it might be mistaken. When we take into account *all* the signals, as in the Keller-Taubman and Plotkin studies, we find that confusions of *5* with *H*, *H* with *S*, *6* with *B*, and *4* with *V* actually do account for about one-fifteenth of the substitution errors. Also, in terms of most frequently confused *pairs* of signals, *6-B*, *5-H*, and *H-S* are among the four top pairs in each study.

Secondly, we might suspect that accurate judgments of auditory number would be related to reaction time, as Saltzman and Garner found for simultaneously shown visual dots. Greater difficulty would then be expected for dot signals later on in training. Quicker reactions would be required as the signals came in ever quicker succession. Finally, it might be that dotting errors would persist for a longer time than other errors.

TABLE 1

RANK ORDERS OF DIFFICULTY IN MASTERING THE ALPHABET SIGNALS OF INTERNATIONAL MORSE CODE (RANKS BASED ON SUBSTITUTION ERRORS ONLY)

Rank	Keller-Taubman	Spragg	Plotkin
1 (most difficult)	W	Y	P
2	P	P	L
3	Y	X	W
4	Q	W	J
5	G	Q	Y
6	L	U	G
7	U	J	F
8	X	F	X
9	C	C	Q
10	D	L	Z
11	J	G	U
12	F	Z	H
13	K	K	D
14	R	R	C
15	Z	D	K
16	H	B	R
17	B	H	B
18	N	A	V
19	S	V	N
20	M	I	O
21	A	N	S
22	O	M	I
23	I	S	M
24	T	T	T
25	V	O	A
26	E	E	E

Support for such thinking as this soon came from an extensive investigation by Seashore and Kurtz,[13] working on a wartime Navy project. These men carried the error analysis into later stages of training in code reception. Classes in Navy code schools were tested periodically with the project's standard proficiency tests.[8] The tests were given at different speed levels beyond basic code training, and all records of 80 per cent accuracy or better were examined for signal confusions. The findings, after 2, 4, 8, and 12 weeks of training showed a fairly constant rank order of difficulty. There was a *low* correlation (+.26) of their rank

* The greater difficulty of *H* in Plotkin's study (as well as the relatively low correlation between the Keller-Taubman and the Plotkin ranks) may be due to the fact that Plotkin took as his measure of difficulty, not the number of errors made on each signal prior to mastery of the entire code, but the number of times each signal was presented before three successive correct responses were made to it.

order with that obtained by Keller and Taubman, and, among the very most difficult signals at each stage of progress, were the following: *6*, *5*, *4*, *B*, *H*, and *V*—all of them 'dot signals.'

In addition to this, the *direction* of error was primarily toward *under-estimation*. Seashore and Kurtz remark that "the most interesting trend seen in the data . . . can be called the *signal-shrinkage phenomenon*, that is, a tendency for the student to hear code signals as being shorter than they are." They go on to suggest that special attention should be given to those signals that are so hard to copy without error—*6*, *5*, *4*, and so forth. Presumably this might be done in two different ways. We might arrange our practice material so that the "hard" signals came much oftener than the "easy" ones, thus giving our student more chance to practice on them. Or we might give special drills on the trouble makers, to sharpen the distinctions between them in the routine transmissions. Both possibilities have since been explored.

E. A. Jerome[4] examined test papers in a Signal corps school for high-speed operators. He found that most of the failures to pass the daily tests were due to the same sort of confusions as noted by Seashore and Kurtz. "Remedial" drills were therefore constructed and given to certain students in an attempt to eliminate these errors. The drill material included such five-letter cipher groups as *HHSSH*, *BDBBD*, *etc.*, and was used during one of the four daily hours of receiving practice. Result: the "remedial" device was not remedial, no advantage whatever accrued from the drill. Indeed, if the drill was carried on for more than a couple of weeks, it was harmful in its effect.

Within the past year, Sidman[14] compared the progress of two groups of beginners in receiving code. One group used as its practice material an equal frequency of all the signals, both letters and digits. The other group used material that was weighted for signal frequency in accordance with the supposed relative difficulty of the signals. The data from this study have not yet been closely scrutinized, but it is clearly to be seen that no difference in group progress occurred as a result of the different practice material.

This schoolroom type of research has had some degree of tie-up with the laboratory. As early as 1943, Jerome had carried out an experiment at Columbia University in which six subjects were asked to judge the number of auditory dots (1 to 16 short tones) at seven different rates (from 3.6 to as high as 20.1 per second). He found that the per cent of correct judgments fell off markedly as the *number* or dots increased or as the *rate* of dotting went up.

Jerome's work, unfortunately, was never published, but his lead was soon followed by Taubman,[16] who had been helping to develop the code-voice method of training. Taubman had been impressed by the way in which immediate knowledge of response correctness had seemed to aid code learning, so he undertook to make a special study of its effect upon the dotting error. He asked his subjects to judge from 1 to 6 short tones (like those in Jerome's study) at rates of approximately 7, 8, and 9 dots per second. Four of his subjects were told, after each judgment, the correct number of dots, while three others worked without such knowledge. Both groups improved during their period of training, but the "reinforced" group was distinctly superior, in terms of mean *judged number* and mean *per cent correct*. All subjects underestimated dot number from beginning to end of the experiment, but *over*-estimation also appeared in the case of those subjects who worked with knowledge of their correctness. Taubman treated this as a compensatory effect arising from the subjects' awareness that they commonly erred in the opposite direction.

From this pilot study, Taubman went on, after the war, to a larger-scale investigation of judged number, visual as well as auditory.[17] In alternate practice sessions, short tones and short flashes of light were presented to subjects at five different rates. The number ranged from 1 to 10. The auditory rates were from 6 to 9 per second, approximately, and the visual rates were from 2 to 5. Each subject judged each stimulus number at each rate 25 times.

Again the results showed that the accuracy of judging number decreases with (1) an increase in the stimulus number and (2) an increase in the rate. The more the dots, or the faster they come, the less the accuracy. The error is, once more, an error of *under-*, rather than *over-*, estimation. And now we know that these findings are not restricted to auditory dots alone, they hold for visual dots as well.

Taubman's data thus support his own earlier observations. They support Jerome's observations and they support those made by Hall and Jastrow 67 years ago. But this is not all. They have in turn been supported, and extended, by two further investigations, one of which was made, appro-

priately, at Johns Hopkins, where the experiments began.

W. R. Garner[3] employed short tones, of two intensities and two durations, and from 1 to 20 in number. He presented these tones at five different rates: 4, 6, 8, 10, and 12 per second. His data show again the effect of rate and number upon accuracy of judgment, with the same error of under-estimation. (No influence of tonal intensity or duration appeared.) He did, however, note one factor not previously emphasized, that of wide individual differences. Some of his subjects could not count accurately more than four successive tones even at a repetition rate of four per second ". . . The best quarter of the group could count as accurately at a rate of eight per second as the poorest quarter could at a rate of four per second."

The second follow-up of Taubman's study was in an experiment by Cheatham and White,[1] in the U. S. Navy Electronics Laboratory. These investigators went beyond Taubman's highest rate of 5 dots per second to rates of 10, 15, 22.5, and 30 per second of light flashes, and had subjects judge from 1 to 20 flashes at each rate. Once more number and rate are reflected in erroneous response, and there is still a striking under-estimation of number, even for two flashes when the rate is high. But something new comes in. The relation between judged number and stimulus number shows rather well-defined steps. This is especially true when the flashes come at a rate of 30 per second. At this rate, 4 and 5 flashes will generally be reported as *two*; 8, 9, or 10 flashes will be reported as three; 14 and 15 will be called *four* and 18 and 19 will usually be called *five*. Other, intermediate, flash numbers will be divided between these judgment categories. Surprisingly enough, the judgments of number were made *easily* and *consistently*. Thus, when 9 flashes were presented at a 30-per-second rate, a subject might report that he saw three clear and distinct flashes. More accurately, there were three *pulsations*—expansions and contractions of light such as those described by Kenkel in 1913 and called "gamma movement." According to Cheatham and White, this reported number is "dependent on both the number of flashes presented and the total time in which they are presented."

Here, then, is a new development. It will undoubtedly receive further experimental attention and be related in due time to other visual phenomena. In addition, it may eventually bear upon the comparatively neglected practical problem of receiving Morse code when it is transmitted by blinker. Visual code reception may be more than a slowed-down version of auditory code reception.

These are the only research data that I have to report at this time on the problem of judging stimulus number. Before leaving the problem, however, I would like to consider it briefly in a different context.

Accurate reports of stimulus number and accurate reactions to Morse code signals are basically matters of stimulus discrimination. On this I think we would all agree. In responding adequately to the code signals, a student must make at least 36 different responses, one for each of the 36 different stimuli. However, as in the case of many discriminations within a single sense modality, these stimuli, at the start of training, are easily confused with one another. When we increase the probability of a specific response to one stimulus, we also increase the probability of the same response to another stimulus. This is done on the basis of whatever properties the two stimuli share between them. For example: when we strengthen the response "C" to the signal for *C*, we also strengthen, to a lesser degree, the response "C" to the signal for *V*. And so on. This is what, in present-day behavioral terms, we call "generalization." Learning to tell the signals apart requires the *breakdown* of many such generalizations.

The breakdown of generalization is achieved for most of the Morse code signals in perhaps 8 or 10 hours of practice. One little cluster of signals may, however, hold out much longer than the rest. The signals for *6*, *5*, and *4* persist in arousing the responses for *B*, *H*, and *V* respectively. In like manner, the signals for *B*, *H*, and *V* are sometimes mistaken for those belonging to *D*, *S*, and *U*. The *gradient* of generalization, we might say, extends primarily in one direction and for 'one dot' only. At least this is the case when the total number of dots is no more than four or five, and when the rate of dotting is not excessive.

This leads me to mention one further experimental study, by Kaufman, Lord, Reese, and Volkmann,[5] at Mount Holyoke College. In this study, subjects were presented briefly with visual patterns of dots, from 1 to 210 in number, and asked to report the number as quickly and as accurately as they could. This is the modern form of the Hamilton or Jevons type of experiment.

One of the important findings of this study was a sharp discontinuity in the functions relating stimu-

lus number to the time required for report, and to the confidence with which the report was made. In both cases, the break in the curves appeared at the same place—close to the point for *six stimulus dots*. This discontinuity led Kaufman and her associates to a distinction between three kinds of discriminative judgment: *estimating*, *subitizing*, and *counting*. *Estimating* is treated as a report of numerousness when the stimulus number is greater than six. *Subitizing* (from the Latin, *subitare, to arrive suddenly*) is applied to the discrimination of six, or less than six, stimuli. *Counting* is said to occur "when the stimulus-dots are presented in one place at a sufficiently low rate; when they are simultaneously presented in different places and are kept there; when they appear successively, in different places, and at a low rate." They point out that, in counting, a person makes one response for each one of a group of N objects, whereas, in subitizing or estimating, a single response is given to an entire group of N objects.

In relation to the experiments that I have reviewed here, all three of these processes have probably been involved at one place or another. In some cases, where rates have been very slow, *counting* has undoubtedly occurred. In others, particularly when high dot numbers have been used, there must have been *estimating*. With high speed and low dot number, *subitizing* has probably been the rule. This is perhaps the usual case with Morse code, where the signal number does not exceed five dots and the speed is often too fast for counting.

Subitizing does not, unfortunately, guarantee accuracy. We have seen that even as few as two or three dots may be underestimated if the rate is high; and five may be called four, even with low rates. Moreover, there are wide individual differences. This point was made by Garner, and may be confirmed in any code school. There are some trainees who will err in judging number when the rate is that of manual tapping, others will subitize successfully at rates much higher. Small as this generalization gradient may be, it cannot be eliminated by any known method of training. We seem to be dealing with a threshold problem, sometimes a very upsetting one. And, as in the Pavlovian case, we may find 'neurotic' symptoms in our students as they approach the peak of their performance. "Code neurosis," a term that grew up in the training camps of the last war, is not an empty phrase.

These individual differences suggest, at the practical level of Morse-code learning, that we might well construct a test of code aptitude that would take them into account. This is a real possibility. It was partially recognized by Thurstone,[19] in 1943, but was laid aside before it had been fully explored. It has also been suggested in two or three of the papers I have cited in this talk. Within the past year, in fact, a preliminary form of such a device has been tried out on a small scale, with results that seem to warrant further work in this direction.

Still another possibility has been suggested by one or two workers in this field—most forcibly, and most recently, by Taubman.[17] It is unlikely that this possibility will ever be realized, but it would certainly not take more than one large-scale piece of institutional research to decide upon its practicability. The proposal, simply stated, is this: *Why not change the International Morse code?* Why not, in the interest of easy and effective communication, replace three signals of the code and thereby eliminate most of the discriminative problems associated with it? The three signals, of course, would be those for the letters *B*, *H*, and *V*, the letters that stand squarely in the trouble-making spot between *6*, *5*, and *4*, on the one hand, and *D*, *S*, and *U* on the other. Take away these three offenders and you would at the same time take away most of the pain involved in acquiring and employing the International Morse code!

There are three especially good candidates for these positions. They are:

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Each is a four component signal that could easily be relieved from any duty in communication that it now performs. Each would assuredly be confused to some extent with one or more other signals during the code-learning process, but the discriminative problems that they raised would almost certainly not be lasting ones. And, anyhow, the wisdom of using them, and the manner of introducing them to radio operators throughout the world, could easily be tested in advance, at no great cost, in a suitably designed experiment. Samuel Morse altered his code twice within ten years. Another, fairly extensive, change has been made in it during the past century. There is no need to close our minds forever to the possibility of still another.

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SECTION OF MATHEMATICS AND ENGINEERING

HYDRAULIC RESEARCH—PAST AND PRESENT*

By CHILTON A. WRIGHT†

Hydraulics of the Ancients. It was Archimedes in the 3rd Century B.C. who said that we know more about the laws controlling the movement of the heavenly bodies than those controlling the flow of fluids on this earth. This is still quite true today.

The purpose of this paper is to pursue the science of hydraulics from its earliest beginnings to our present knowledge.[1] For the first three thousand years the fluid most widely used was water, although in recent years the development has been extended to industrial liquids.

There are records showing that, about 1500 B.C., in Mesopotamia, there was an operating water-carriage sewerage system constructed of earthen pipes with flow in both vertical and horizontal directions. About 2000 B.C., there was an artificial water supply reservoir called Lake Moeris, which was fed from the Nile River by the Canal of Joseph. Records also show that chain-and-bucket pumps were used for the drawing of water supply from wells. One of the earliest applications of hydraulics was the use of water for irrigation. In several countries, notably India and China, a self-operating irrigation pumping wheel was developed.

About 1400 B.C., the Egyptians developed a water clock, very similar to an hour glass, consisting of a vessel with an orifice in the bottom and the cross section varying so that the drop of the surface was directly proportional to the elapsed time. From this period until the Roman period, all knowledge seems to have been lost.

Roman Period. About 250 B.C., Archimedes developed his laws of flotation. In the Roman period, about the beginning of the Christian Era, a wealth of scientific hydraulic knowledge was shown by the construction of grade line aqueducts with valley crossings of lead pipe (inverted siphon) and of water supply distribution systems to 1200 fountains in the city of Rome and many baths and reservoirs. About 100 A.D., Frontius, the Chief Engineer of the City of Rome, wrote about engineering factors of the water supply. Following the fall of the Roman empire, the hydraulic knowledge again became lost for about one thousand

* This paper, illustrated with lantern slides and a motion picture, was presented at a meeting of the Section on March 20, 1953.

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years; possibly because very few people were able to read and write.

Canal Building Era. It was not until 1500 A.D. that the modern science of hydraulics began with the writings of Leonardo Da Vinci, the noted scientist of that time, whose versatility was shown by his achievements as a master painter as well. This was called the canal building era and the developments in hydraulics were shown by the construction of a number of interconnected canals throughout parts of Europe.

In 1612, Galileo developed his hydrostatic paradox which demonstrated that the pressure on a submerged surface is independent of the actual volume of water, and depends only on the depth.

In 1644, Torricelli developed the orifice law, which proved that the velocity is proportional to the square root of the head, that is $v = \sqrt{2gh}$.

In 1650, Pascal's law was developed showing that fluid pressure is transmitted freely in all directions and is equal to the depth multiplied by the specific weight of the fluid.

In 1684, Marcotte experimented with the development of flow through tubes and orifices.

In 1690, Guglielmini, in his treatise on measuring water, developed an interesting but erroneous theory of river flow. He assumed that the velocity distribution in the river was proportional to the $\sqrt{\text{depth}}$, thus obtaining the maximum on the bottom. The fact that his theory was adopted by many writers of his time shows the extreme lack of correlation between theory and experiment.

In 1730, Pitot first measured the velocity of a fluid by means of an open impact tube in which the height of the fluid was proportional to the square of the velocity.

In 1738, Bernoulli developed Bernoulli's theorem, known as the conservation of energy, and expressed as $\frac{V^2}{2g} + \frac{P}{w} + z = \text{constant}$.

In 1757, Brahms developed the relation between velocity and slope for rivers, later made definite by Chezy in 1775, i.e., $V = C \times \sqrt{RS}$.

Hydraulic Laboratory Investigations. After about 1775, the development was very rapid in the science of hydraulics with a number of scientists developing laws and formulas now used.

In 1779 Dubuat developed the weir formula $Q = CLH^{3/2}$ later brought into wide use by James B. Francis as the Francis formula: $Q = 3.33LH^{3/2}$ (for sharp crested weirs).

In 1784 Venturi experimented with flow through diverging tubes which later became perfected by Hershel and the device is now known as the Venturi Meter.

In 1828 Belanger developed the hydraulic jump, which was made practical by Woodward in 1916 and is now widely used for dissipating energy at the bottom of spillway dams.

In 1832 Poncelet and Lebros made elaborate experiments on orifice flow which are still used today.

In 1842 Poiseuille and Hagen developed the formula for flow through small tubes and for laminar flow, now known as Poiseuille's formula.

In 1845 Darcy, Eytelwein, Fanning and Weisbach developed the pipe friction formula $H_f = f \frac{L}{d} \frac{V^2}{2g}$ now widely used in fluid flow in pipes.

In 1849 Stokes experimented with particles falling through fluids giving rise to what is known as Stokes' law: $V = \frac{D^2(w_p - w)}{18\mu}$.

In 1869 Ganguillet and Kutter developed what is now known as Kutters value of Chezy's "C" for flow in open channels.

In 1883 Reynolds experimented with dye-threads in pipe flow and developed the flow criterion called "Reynolds number."

In 1890 Manning improved the formula for flow in open channels by making it the simpler form: $V = \frac{1.486}{n} R^{2/3}S.^{1/2}$

Around 1900 the activity of the New York City Board of Water Supply in developing a long range plan for water supply of New York City stimulated interest in hydraulic engineering and the era of model testing began to dawn. One of the earliest hydraulic models was made by B. F. Groat (1917). It was a small scale model of a hydro-electric project in which the movement of chunks of ice was simulated by paraffin cubes. It was realized about this time that the action of water in various hydraulic structures and machines was somewhat unpredictable and tremendous expansion of hydraulic laboratories took place in which these properties were studied by means of hydraulic models. Many laboratories were built in Europe and America.

In 1929 John R. Freeman was instrumental in publishing (A.S.M.E.) a book called Hydraulic Laboratory Practice, summarizing the methods of model testing in both Europe and America. He

established the Freeman Fellowships for study of Hydraulics in Europe and the dissemination of hydraulic information. In this country the universities enlarged their hydraulic laboratories. A National Hydraulic Laboratory was established at the Bureau of Standards, Army engineers built a large outdoor laboratory at Vicksburg, Mississippi, at which the study of large scale models of rivers was carried on. Some of the Mississippi River models covered many acres, and studied such problems as the effect of removing obstacles in the river bed upon the flow. One such model was of the East river at Hell Gate, leading to its improvement by dredging.

About this time an attempt was made to analyze the motion of fluids by dissecting them with the aid of injected dye and high speed motion pictures. It was found that the flow of fluids was influenced by the degree of turbulence in the stream and the names of Bachkmeteff,[2] Von Karman, Prandtl, Nikuradze, Dryden, Rouse, Kalinskee,[3] and many others were prominent in developing theories of turbulence. Several theories regarding this transfer of internal fluid energy into heat have been advanced but have been worked out only for smooth pipes. The evaluation of turbulence and its relation to loss of energy, usually called friction, is still a challenge to the investigator.

At the present time, according to the Bulletin of Hydraulic Research in the United States issued by the National Bureau of Standards, there are 60 institutions, 33 laboratories of the government departments, and 60 foreign hydraulic laboratories engaged in pursuing a multiplicity of problems in hydraulic research. These problems vary from the study of rainfall, to problems of the hydraulic properties of the soil, operation of hydraulic machines, cavitation in pumps and turbines, construction of river control structures, and apparatus to demonstrate very obscure fluid laws. There is no time to go further into detail with these projects, but those interested can consult this bulletin and another, Bulletin of International Hydraulic Research.

Polytechnic Institute. Several departments of the Institute conduct fluid research, but there is only time to give a few illustrations from the Hydraulic Laboratory.

The characteristics of laminar flow of fluid in a small glass pipe have been investigated, and a unique apparatus developed by Messrs. Pue, Shoenhaar, and DeCicco, working at different times. The apparatus consists of flow of oil through a small glass pipe in which both laminar and turbulent flow can be produced by heating the oil.

One of the least known properties of fluids is its resistance to flow down a steep chute. Mr. Stewart has investigated this by means of an adjustable slope, transparent flume, constructed of pyralin.

Lock-Filling Culvert. Twin filling culverts were desired to fill a large dry dock in one hour. The water was to be brought up through the floor of the dock at the upper end as evenly as possible across the whole width. On account of the curves in the filling culvert it was felt advisable to check the computed results by means of a model test, and a small model was made on a scale 1:24. The trash racks were simulated by means of wire mesh screens. After a number of trials a uniform distribution of flow was obtained from each port.

Fluid Polariscope. An apparatus for illustrating the nature of fluid flow is called a fluid polariscope. A special solution is sent through narrow passages and by means of polarized light the lines of fluid flow can be seen.

Loiza River Dam. In the construction of large spillway dams there is usually a large amount of excess energy present in the over-flowing water moving at high speed at the bottom of the toe of the dam. If it is not dissipated by some means it will rapidly wash out the dam and the dam will be there no longer. For the case of the Loiza River Dam in Puerto Rico a desirable method of construction was determined by studies and model tests in the glass-walled flume in the Polytechnic Hydraulic Laboratory. The proposed dam is to be 55 ft. high, to carry 100,000 cubic feet per second of water. The model was made with the dimensions in the ratio of 1:48 scale. The river bed was simulated in the laboratory by means of a fine gravel. The record of the results was made by means of pictures showing the depths and scour in the river due to maximum flood conditions. The progress of the test was recorded by means of motion pictures.

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*SECTION OF ANTHROPOLOGY**

THE CULTURAL MAP OF WEST AFRICA: SUCCESSIVE ADAPTATIONS TO TROPICAL FORESTS AND GRASSLANDS†

By DARYLL FORDE‡

Beyond the desert lands of the Western Sahara, and some 1500 miles distant from the Mediterranean coastlands of North Africa are the basins of the lower Senegal and middle Niger rivers and of Lake Chad. From their northern margins and extending southward for nearly a thousand miles again to the Guinea coast which faces the Atlantic to the south is a western segment of tropical Africa that has long stood out in western minds. Vague stories of its torrid heat and its black peoples reached the Roman World. Medieval traders in the Mediterranean heard of its resources and obtained some of the products through the Arabs of North Africa and in the 16th century, with the Age of Discovery, it was brought earlier and more clearly within the knowledge of the West than any other part of trans-Saharan Africa.

This knowledge came from two very different sources and concerned quite distinct parts of this great tract of country between the desert and sea. On the one hand there were the chronicles of medieval Arab travelers, teachers, merchants and adventurers who had, from the 10th century, made the journey of many weeks across the deserts to reach the savanna lands of the western Sudan. On the other hand European merchant adventurers were now making regular sea voyages past Cape Verde, round the western bulge of Africa to establish trading posts where the rain forests of the south came down to the shore on the surf-beaten Guinea coast.

Although European acquaintance with this area goes back a long way, detailed knowledge of its conditions and resources of its peoples and their ways of life is very recent and still sadly incomplete. It was not until the end of last century that western penetration of the interior for pacification and the extension of commerce began. Indeed, we owe a great debt to a generation of scholars of that time, most of them French and British administrators, among whom there still existed the direct and personal interest in the character and traditions of the people they governed and a sense of obligation, as an important part of their public duty, to record and study what they could concerning the peoples among whom they worked. Although the pace of linguistic, ethnographic and historical research has in recent years quickened again in this as in other parts of Africa, the sources for their study are being carried away ever more rapidly by the tide of Westernization. This is happening, moreover, at a time when our knowledge in all these fields, and the insight it could afford to those responsible for administration and development in increasingly complex circumstances, remains fragmentary and often unmeaningful to all but a few specialists. This must be my excuse for attempting, from fragmentary knowledge, to portray the broad features of the cultural map of West Africa and the forces that appear to have affected its delineation.

The older documents of Arab and European travelers; linguistic studies, which for many of the hundreds of West African languages are forced to rely on nothing more than incomplete wordlists recorded by amateurs; preliminary ethnographic surveys of a few regions and a handful of intensive professional studies of the cultures and social systems of particular peoples; these are the materials with which, in our present state of ignorance, any such attempt must be made. But obviously tentative and oversimplified as any such sketch must be, it has its uses in affording those with interest in the peoples of West Africa, whether general or specialized, scientific or practical, a provisional frame of reference against which the wider significance of their more special concerns can be viewed. It will also, I hope, point to the fact that more adequate resources, in research funds and trained specialists, are urgently needed for cultural studies in this important area; that given these there is every promise that the provisional and incomplete outline which it is possible to give today may be developed into a considerable body of systematic knowledge concerning the complex phases and conditions of cultural development in West Africa.

Between Dakar on Cape Verde in the west and Lake Chad nearly 3000 miles away to the east there extends south of the Sahara the belt

* The Section of Oceanography and Meteorology held a meeting on March 24, 1953 at which a paper, entitled, "Meteorological Uses of Airborne Radar," was read by M. G. Beard. No abstract of this paper had been received at the time of publication.

† This paper was presented at the meeting of the Section on March 23, 1953.

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of wooded grasslands nearly a thousand miles deep at its widest, which is generally known as the Western Sudan. At their most characteristic these tropical savannas are fittingly described as orchard bush, covered as they are with waist high grass during the summer rains and closely studded with low trees. Towards the north in the latitude of the lower Senegal river, the bend of the middle Niger and Lake Chad, the vegetation dwindles, trees are sparser and more and more replaced by thorn bushes while the grass cover is low, thin and shortlived, and gives way to the stretches of bare rock and sand that constitute so much of the Sahara desert. On its southern margin the grass and woodland of the savanna become taller and more dense. The country is seamed by belts of forest along flooded river valleys. It merges insensibly southward into a belt of country some two hundred miles deep behind the Guinea coast which, but for the interference of man, would be almost continuous forest.

This gradation of climate and vegetation from the humid forest belt along the coast, which may be drenched in a hundred inches of rain over eight or nine months of the year, to the desert margin nearly a thousand miles away to the north, where there is only a brief flush of short grass during two or three months of showers and storms each year, gives a belt-like character to the West African environment. Although their extent may be modified and even interrupted locally by special features of the terrain, the successive zones of rain forest, open woodland, grass and scrub characteristically succeed one another from south to north as one moves from the coast to the Sahara. Equally significant from the point of view of the spread of different patterns of human settlement and cultural adaptation, each zone extends laterally for enormous distances from east to west and continues still further eastward across Africa. It will be clear that in West Africa there have always been marked contrasts between these zones in the opportunities they have afforded for human movement and settlement, for cultural elaboration and diffusion.[1]

These distinctive life zones of West Africa severally link it to adjacent regions of Africa. The forest belt continues without interruption eastwards across the northern part of the Congo basin; the orchard bush and scrublands in the western Sudan also extend eastwards beyond Lake Chad across the continent to the valley of the Nile and the Ethiopian highlands. Finally there is no sharp line at which the Sahara begins, for within that desertic region, thanks to elevated massifs and raised water tables there are tracts, like the Air and the Hoggar massifs and parts of the Atlantic coast zone, where seasonal herbage and opportunities for primitive irrigation and herding have sustained human settlement and movement throughout the centuries.

Beyond the desert to the north lie the Mediterranean lands of North Africa that lay on the western flank of the ancient civilizations of the Near East, were afterwards developed and organized on a large scale by the Romans and, later still in the first millenium A.D., became the western lands, the Mahgreb, of the Mohammedan Arab world. The Sahara was, as we shall see, no complete barrier between tropical West Africa and North Africa in Ancient or Medieval times. Despite its size and aridity it included a number of tracts that were permanently settled, wider areas over which seasonal pasture was available and lines of water holes along which caravans could water men and beasts. It was thus a hurdle and filter that restricted and selected the kinds of human movement and cultural forces that could penetrate and the sort of influence they could exert on the established populations.

With the opening of the Western Age of Discovery at the end of the 15th century, the Sahara was outflanked by sea. The exploring navigators were followed by sea traders along the southern coasts of West Africa, and the first great stretch of well watered tropical African coast became dotted with the trading posts of European merchant adventurers. The surf-beaten beaches that had so long presented an ultimate frontier to settlement for the peoples of the forests of West Africa were breached and direct contact was established with the expanding mercantile civilization of the west. Western knowledge of this region was no longer confined to classical allusions to a land of Pactolus and to translations of Arab chronicles concerning strange empires beyond the desert. The lure of gold, ivory and slaves brought traders from all parts of Western Europe to the fever-stricken lagoons which later became ports of entry to the interior and, with the opening of this century, the bases from which a new and contemporary phase of cultural change is sweeping over West Africa.

The fact that the peoples of West Africa are

predominantly negroid in racial type is the first general indication that their oldest cultural traditions are, with those of the rest of trans-Saharan Africa, likely to be distinct from those of the Mediterranean and European world. And this is confirmed by the character and distribution of languages, those unwitting and perduring indicators of a substantial element in the cultural traditions of peoples. Very few of the hundred or more languages of West Africa have been studied in detail, but it is already clear that except in the southern Africa. Ultimately then, despite great local differences, which betoken centuries of separation of different regions and considerable extraneous influences, the forest and savanna zones have elements of a common tradition that one would expect to find expressed in other archaic features of their culture (see FIGURE 1).

There is, however, as has been mentioned, a notable exception in the country east of the middle Niger where Chadic languages of the Hamito-Semitic family that form part of a widespread group

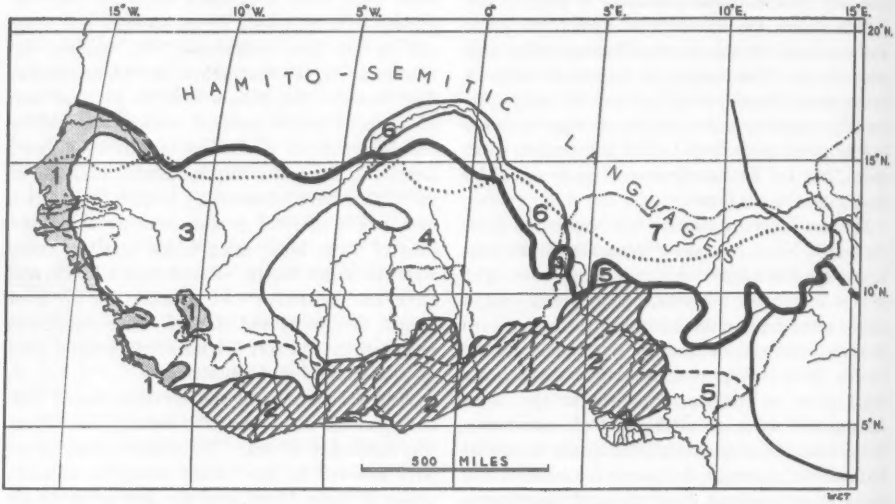

FIGURE 1. Distribution of major language groups in West Africa (generalized). Smaller groups are omitted.

Western Sudanic Group *West Atlantic*.....1. *Kwa-Krus*.....2. *Mande*.....3. *Gur (Voltaic)*.....4.
Benue-Cross and Bantu Groups.....5. Songhai Group (unclassified).....6.
Chado-Hamitic Group.....7.
Northern limit of Western Sudanic Languages.....
Northern margin of Dense Forest.....
Northern margin of Savanna.....

north-east between the Niger and Lake Chad, all the known forms of speech of both the forest and the savanna zones belong ultimately to a single great group of languages, commonly known as the Western Sudanic family. To this group belong linguistically all the West African peoples south of a line running from the west coast at about the Senegal river along the parallel 15° N. to cut across the great bend of the Niger and curve south below Lake Chad. There are indications, too, that further study will link them in a still wider grouping to include the Bantu forms of speech that are spread so widely over central and extending over the Western Sahara and North Africa have spread deeply into the savanna belt. Still further east in the country close to Lake Chad the languages belong to a distinctive Central Saharan group. Human movements from the north in this area, it would appear, have not been confined only to small bodies of people but to have been sufficiently great and pervasive to displace the Western Sudanic tongues that probably preceded them.[2]

Within the Western Sudanic language area there are further points of distribution, that are significant for the early peopling of West Africa.

In the difficult and, for landsmen, inaccessible mangrove swamps of the coastal lagoons of the Ivory Coast and the Niger delta there are small populations whose languages are very distinctive and divergent from the more widespread linguistic groups that surround them. These comparatively isolated fishing peoples in their remote situations may, like other isolated and divergent groups, such as those found in the hills of Togoland, be survivors of once more widely spread linguistic stocks—the equivalent of such linguistic survivals as Erse and Gaelic on the Atlantic fringes of Europe —and it is unfortunate that so far no close study of these remnant peoples has been made. But the greater part of the forest belt of West Africa over a distance of a thousand miles from central Liberia to beyond the lower Niger in Nigeria is occupied by peoples speaking a series of related languages to which the general name Kwa, the common root for "people," has been given. Although the actual forms of speech differ greatly over this area and distinct tongues, unintelligible to outsiders may be confined in places to a few thousand people, there are underlying similarities in vocabulary and structure that indicate their derivation from a common ancient speech and point to an early cultural continuum over much of the forest belt, it suggests the proliferation through it of communities derived from a single stock at an early but unknown date. It points, too, to the obstacles which the forest imposed on penetration by later peoples. That such penetrations occurred, and with profound effects, is clear. They would appear, however, not to have been mass migrations but confined to small if dominant groups which despite great cultural influence were absorbed linguistically by the local populations. Even where, as among the Yoruba-speaking peoples of Southwest Nigeria or the Akan of the southern Gold and Ivory coasts, more complex cultures marked by high technical skills and ritually elaborate state organizations of northern provenience were established, the ancient forest tongues persisted.

In the far west of the forest belt, however, northerners penetrated in large numbers, establishing warrior chiefdoms, as among the Mende of Sierra Leone, which carried Mande languages from the western Sudan right down to the coast. At the eastern end, the forest and adjacent savanna of the Cross and Benue river basins appear to belong to another series of forest tongues. These congeries of little studied class languages may, it is claimed, prove to have diverged from one or more closely related stocks from which the Bantu languages of the Congo basin and beyond also derive. Thus there is no sharp linguistic frontier in the forest zone between West and Central Africa.

In the savanna belt linguistic groupings and their distributions suggest a different cultural situation, one of large scale prolonged movements of culturally dominant populations over great tracts of country. Except in the north-east towards Chad the languages are again all West Sudanic, showing ultimate derivation from the same stock as the forest tongues, but, it would appear, long separated from these. We should look therefore for an early phase of separation of the forest and savanna zones into distinct cultural spheres within each of which there was more internal interconnection than there was interchange between one zone and the other.

Secondly it is to be noted that the West Sudanic languages in the savanna zone do not fall predominantly into a single major sub-group but are divided into a number of divergent stocks each, broadly speaking, occupying a compact block of country extending across the zone from the desert to the forest margin. In the west along the Atlantic there is an area of internally strongly differentiated languages—the West Atlantic group — suggestive of the early entry and proliferation of a number of comparatively self contained populations. That the area they once occupied has been reduced and interrupted by later migrations and cultural influences from the East is shown by the many islands of West Atlantic speech persisting to the East where the widespread group of Mande languages predominate over the upper basins of the Senegal and Niger rivers. The Mande speaking peoples (such as the Mandingka and the Bambara of Senegal and French Sudan; and the Mende of Sierra Leone and Western Liberia) share a tradition of centralized military organization under strong chiefs. They were still expanding in the west and south when European pacification began. Moreover, the general distribution of the Mande tongues corresponds broadly to the sphere of influence of a vigorous civilization that, according to the Arab chronicles, was already flourishing early in the Christian era in this part of the Western Sudan.

East of the area of the Mande languages there is

another body of peoples occupying nearly all of the great tract of savanna country south of the Niger bend who speak various languages of the Gur or Voltaic group. These peoples vary greatly in complexity of culture and scale of social organization for, as we shall see, they were situated on the flanks of powerful early kingdoms lying to the west and north and while the more remote remained isolated in small independent communities others, like the Mossi, while retaining their old languages became organized in military chiefdoms after the model of their dominant neighbors.

East again we enter the area of a distinct language family, an area of Chadic speech occupying much of what is now Northern Nigeria and the French territory that flanks it to the north. Most of this area was early organized into a number of strong chiefdoms which by their traditions and their continuing commercial and other connections were linked to the oasis peoples of the Western Sahara.

Thus the linguistic distributions in West Africa suggest several important underlying features of cultural development. First, since apart from the Saharan extensions into the savanna around Lake Chad, all the languages of West Africa appear to be ultimately derived from a common stock, one would expect to find significant elements of a common early tradition in the cultures of all West African peoples. Little systematic enquiry has so far been given to this question but there are many indications that underlying the great regional and tribal differences in the elaboration of cult and cosmological ideas there is a very widespread substratum of basic ideas that persists in the rituals, myths and folk tales of West African peoples.

On the other hand the tendency of linguistic frontiers to correspond with the savanna–forest nargin suggests an early and important cultural differentiation between these two zones. In the savanna, where until recently the human movement over considerable distances was so much easier than in the forest we find that a series of distinct sub-groups have expanded over compact areas. The resulting marked differentiation of the major linguistic stocks in the savanna belt would appear at first sight to conflict with the fact that the country is so much more open and so more favorable to human movements under primitive conditions but here it is to be noted that the several major stocks are not confined to small areas or populations. The savanna zone is far wider than the forest and the area over which the Mande languages for example, are spoken is at least as great as that covered by those of the Kwa group in the forest zone. It is to be noted also that there are far flung outliers of Mande speech as far east as Nigeria. What appears to be significant is the emergence of a number of distinct foci of linguistic differentiation in this wide, deep zone which severally expanded transversely across the savanna as also, at a presumably later date, did the intrusive Hamito-Semitic stocks in the east. This configuration of language groupings is of particular interest in connection with what we know of the early political framework of the Western Sudan, where a series of elaborate political systems such as the Gana and Mande empires and their succession states and off-shoots in the west, the Dja, Songhai and Mossi Kingdoms in the centre and the Hausa states in the east appear to have maintained their structural identities over the centuries. We reach the provisional conclusion that the grasslands of the Western Sudan covered too vast an area and was too open to distinct external influences on too long a front for it to retain or to have imposed on it by migration or conquest any complete linguistic or cultural homogeneity. At the same time the more open character of this country made it possible for expanding ruling groups to maintain partial unity, linguistic, cultural and political, over very extensive areas.

When we turn to consider the indigenous modes of subsistence of the known peoples of West Africa we again find a general, though by no means complete, dichotomy between the forest and the savanna peoples.* If we abstract from the cultures and social systems of the forest peoples those elements which appear to have developed following maritime contact with the west, including new food plants such as maize and cassava, and if we also exclude, for the moment, certain more complex societies of the forest zone that afford evidence of northern origins, the broad features are as follows: The forest peoples were and are cultivators depending basically on root crops, yams (*Dioscorea*) and cocoyams (*Colocasia esculenta*), and fruits,

* Archeological research in West Africa has not advanced sufficiently to attempt any comprehensive regional or culture-sequence interpretations, or to yield much evidence concerning pre-agricultural peoples. It must be recognized, however, that the ancestors of the present language stocks may well have been first introduced by foraging and hunting peoples before the introduction of crops.

especially varieties of the cultivated banana (*Musa* spp.). These are supplemented by a variety of legumes and supplies from cultivated or protected bushes and trees notably the oil and raphia palms, pepper bushes and the cola tree. Stock-raising, hunting and trapping, although much reduced recently, was prominent in the traditional economy but livestock was and is confined to small numbers of goats, fowl, and pigs attached to the household.* Their fabrics were confined to pandanus and raphia matting and bark cloth and they had no true loom. Iron tools were generally available but often only through trade since the centers of ore-smelting as distinct from the smithing of iron bars were comparatively few. With iron tools they had well developed wood working crafts serving both utilitarian, ritual and esthetic ends with such products as stools, slit gongs, large assembly houses, statuary and masks. Pottery was generally available but it, too, was often traded at considerable distances from specialized centers of surplus production.

The older cultivated food staples of the West African forest belt are also found throughout the great forested areas of central Africa to the east. They undoubtedly reached West Africa from that direction for they are not African plants by origin. The yam (*Dioscorea alata*) and the Coco-yam (= Taro, *Colocasia esculenta*), the banana and the plantains (*Musa*) were all, the botanical evidence indicates, first domesticated in an archaic planting area in southern Asia extending from the Bay of Bengal to Indo-China where agriculture was based not on the sowing of cereals but on vegetative reproduction of food plants from cuttings. The domestic forest goat and the fowl, too, which are ubiquitous in the Guinea-Congo region, were ultimately derived from South Asia. These domesticated plants and animals appear to be part of an ancient craft complex which included matting with pandanus and palm fibres and the beating of bark cloth. The period and the route by which it reached tropical Africa remains unknown but the biological evidence makes it clear that the basic plants and animals concerned are exotic there. The Guinea forest peoples appear, however, to have made an important addition to the assemblage in developing two African yams—the white and yellow Guinea yams (*Dioscorea rotundata* and *cayensis*) as cultivated plants.†

One outstanding exception to the general pattern of indigeneous cultivation in the forest belt is very significant. In the west from the Gambia to Western Liberia, rice, grown both dry and in swamps is a staple crop. None of the early European reports suggested that it was a recent introduction and it was not recorded from anywhere further East at the time of European discovery. Its presence in the west is, therefore, more satisfactorily explained by the fact that rice had long been an important riverain crop on the middle Niger whence, like the southward spread of Mande languages it reached the forest peoples.

As far as they can be judged, from those existing forest peoples who have remained outside the spheres of the more complex state organizations of northern origin or of later developments in response to European commerce, the older patterns of social organization in the forest belt, while variable, were all small in scale and rooted in local ties of kinship. The local community, rarely exceeding a few thousand persons and often only a few hundred strong, was virtually autonomous, with its own organization into groups of kinsfolk and its own system of authority. It had external contacts with similar neighboring groups, intercourse that was sufficient to maintain general similarity of speech, custom and social organization. Beliefs, skills and social innovations could spread widely from one to another and a sense of cultural unity maintained among a considerable number of communities. Their inter-relations were not regulated from above, they took the form of chains of friendships and alliances, liable to be broken by feuds and intermittent hostilities. A lineage system (patrilineal, matrilineal, or even dual) whereby kinsmen in one line of descent maintained solidarity for both internal organization of their own group and for external cooperation and competition with similar groups, appear everywhere to have provided the first order of grouping within a locality. Among some peoples the lineage principle was more widely extended to embrace a series of local communities conceived and organized as a body of kin, segmented into ultimately related groups. Elsewhere, and associated with

* It is only in limited areas that dwarf cattle, ultimately of northern origin, are reared.

† See Burkhill, L. H. 1951. The rise and decline of the greater yam in the service of man. The Adv. Sci. 7: 443 *et seq.* For a general account of the early development of Old World tropical agriculture in South Asia and references to the literature see C. O. Sauer. Agricultural Origins and Dispersals. Bowman Memorial Lectures, Series Two. 1952. Am. Geog. Soc.

peoples living in larger compact settlements comparatively isolated geographically and socially from one another, a village organization, with territorial, age-set and status-associations, is superimposed on the system of kin groups of more restricted significance. Nowhere, except where the extraneous influence of invading minorities is both traditionally asserted and intrinsically probable, were politically centralized states with an administrative and territorial system of government established. The relations between lineage or small clan-organized tribes or between autonomous village communities were those of give and take in trade and intermarriage, punctuated by differences settled through arbitration, feud or warfare.[3]

The savanna peoples show an overall contrast with those of the forest in their subsistence patterns. But it is also apparent that beyond the general contrast in type of cultivation there is great internal variation in technical development. The peoples of the Western Sudan are predominantly grain cultivators as compared with the root and fruit growing forest peoples. But the intensity and technical efficiency of their agriculture ranges widely. Some, like many plateau peoples of Northern Nigeria and perhaps of the Cameroons knew, until recently, only an inferior small grain, *Digitaria*. Others, like the pagan peoples of much of the Northern territories of the Gold Coast, although they cultivated varieties of millet which are widespread and ancient food plants in Africa, merely scratched the soil with light hoes and dibbled in their seed to secure a catch crop. But other savanna peoples such as the Hausa of Northern Nigeria, the Bambara and Mandingka of the of the French Sudan have a much more advanced agriculture practicing deep hoeing and ridge cultivation for their millets and irrigation for special crops. The level of agricultural production whether per head or by area appears to be in general considerably higher and can provide a surplus to maintain specialists in craft, ritual or government. It is only in connection with this more advanced agriculture that cotton is generally grown and true looms are used to provide cotton cloth. Associated with it, too, is the long established tending of livestock either by the people themselves, as in Senegal among the Wolof and Serer, or by specialized pastoralists living in symbiotic relations with the cultivators as do the pastoral Fula among the Bambara in Sudan or among the Hausa in Northern Nigeria.

The various millets, a botanically heterogeneous assemblage of small-seed cereals, which have so long provided the food staples of the West African savanna zone, belong to an agricultural tradition that is quite distinct from that of the root and fruit crops of the forest. Their distribution in Africa and beyond make it quite clear that seed cultivation in the West African grasslands was not historically derived from forest cultivation or vice versa. The genetical and distributional studies of Vavilov and others have also shown that the flanks of the Ethiopian highlands in Northeast Africa must have been an early center for the development of several varieties of cultivated millets and that Guinea corn (*Sorghum vulgare*), *Pennisetum spicatum*, and Eleusine (*E. corocana*) were probably first cultivated there. Thus the early development of agriculture in the Western Sudan must, like that of the forest cultivation, be derived from the east but by a different route.

Although the two traditions were later, following on subsequent interpenetrations, combined on the forest margins they appear to have been originally separate. Agriculture must have spread separately among the early populations of the two zones. And since, as we have seen, the speech families of the forest and the savanna are derived from an ultimate common stock, their early linguistic divergence into distinct forest belt and savanna groups may well have been associated with the introduction of these two distinct patterns of cultivation and the independent growths and westward expansions of populations that they made possible. This question is one that deserves close attention linguistically, ethnographically and archeologically, for data from these three fields may in combination make it possible to learn a great deal concerning the character and antecedents of the first agricultural peoples in West Africa.

But the agricultural patterns of the Western Sudan have also gone through several phases of development as more advanced techniques and additional crops and associated crafts were developed in some areas. Among some of the savanna peoples, as we have seen, there persists a more primitive economy with a less productive agriculture, lacking textiles and other specialized crafts and often dependent on sporadic trade for iron. When we consider the social organization of such peoples we find it broadly similar in character to that of the forest peoples in the high degree of autonomy of small local communities and the

importance of extended kin groups for the organization of social relations within and between them.

The more advanced and productive agricultural systems and the elaboration of specialized crafts in cloth and metal, on the other hand, are associated with a different social order. Such peoples whether Mandingka in the West or Hausa and Kanuri in the East are organized in states, which although they vary greatly in size, have basic features of social organization in common, namely the centralization of authority in a ruler with his councilors and sub-chiefs drawn from an aristocracy of birth; an elaborate etiquette of obeisance, expressive of ranking and subordination of classes in the social order; the collecting of tax and tribute to maintain the central organs of government and its agents. The more primitively organized peoples referred to above have persisted only in areas which have not been dominated and incorporated in these states and one of the processes of incorporation was very apparent when Europeans first penetrated and began to administer the various territories in the Western Sudan. The kin-organized tribes on the periphery of the centralized states were the slave-raiding reservoirs of the former. Only those in the more remote and difficult country remained unmolested.

For many centuries Islam has been the religion of the barbaric states of the Western Sudan. But the records of the Arab Moslem chroniclers, who visited the Western Sudan in medieval times, themselves confirm the later ethnographic evidence that, however great the importance of Islam in reorganizing various Sudanic kingdoms at different periods, their fundamental ideas and customs concerning political rule and other social relations are much older than the introduction of Islam and that elements of older royal rituals and social codes have everywhere persisted in varying degrees.

What, in broad terms, do we know of the formation and the technical and social basis of these ancient chiefdoms and empires? The earliest contemporary records are those of Arab Moslems who crossed the western Sahara, on an already well established trade route from Sigilmassa, then the great desert port of what is now Morocco, to the Senegal. Ibn Haukel in the 10th century A.D. and El Bekir in the 11th century recorded vivid and often detailed impressions of an empire then extending over many thousands of square miles from the upper Senegal to the Upper Niger and southward over the highland country to the forest margins (see FIGURE 2).

The then ruling dynasty of this empire of Gana or Ganata not only claimed an ancestry of several centuries but also succeeded to a still older Kingdom founded by 'white' men from the north. Gana of the 10th century was controlled from a great city, the royal capital. The kingship was a sacred institution and the ruler himself hedged by an elaborated ritual and regarded as possessed of supernatural powers. The state organization with the aid of a standing army controlled a vast area, collecting tribute in kind from the towns and villages of its provinces and its dependent chiefdoms, imposing customs dues on trade and exercising a royal monopoly on the gold production from the auriferous gravels of the southern hill country which appears to have been all-important in promoting and maintaining the trans-Saharan with North Africa. Although we have only tantalizing glimpses of the elaborate court ceremonial and religious ideas of Gana it was clearly not a Moslem state. Moslems from North Africa were tolerated as merchants but they had their own quarters and were not incorporated into the society.

It was not until late in the 11th century that the first recorded attempt at Islamic domination took place with the Almoravid conquest of part of Gana by Moslem berbers. Although the Almoravids did not succeed in establishing their own rule, Islam, continually reinforced we may presume by traffic along the western trans-Saharan trade route, was henceforth powerful in this part of the Western Sudan. The rulers of Mali or Mande, formerly a subordinate chiefdom southwest of Gana, adopted Islam in the 11th century on their rise to power and secured a fluctuating but growing control of much of the former territory of the empire of Gana. Ibn Khaldoun's account of his stay in the capital of Mali, when it was at its zenith in the early part of the 14th century, portrays a state system with a sacred ruler, essentially similar in its main features to Gana, deriving its revenues, directly or indirectly, from the tribute of thousands of peasant villages, grouped in provinces or subordinate chiefdoms. Mali maintained regular commercial, diplomatic and scholarly relations with North Africa and many of its kings made the pilgrimage to Mecca before it dwindled to a petty chiefdom in the 17th century with the rise of new centers of power on the middle Niger to the east.[4]

Although contemporary records do not carry us so far back in the country to the east of the empires Gana and Mali, there is much indirect evidence of the early establishment of pre-Islamic Kingdoms in the country of the Niger bend and further east across the northern savanna from the Niger to Lake Chad. As both of these regions were in later times in contact with North Africa across the Sahara by other caravan routes and since, as we have seen, part of it became an area of Hamitic speech it is likely that infiltration of these parts of the western Sudan by northerners also ascribed its original rulers to invaders from the Saharan oases of Air long the home of Hamitic speaking Berber peoples. Similarly the foundation of Kanem, the forerunner of the latter-day chiefdom of Bornu, was attributed by medieval Arab chronicles to invaders from Tibesti in the central Sahara.

The widespread conversion to Islam of the rulers of the many chiefdoms and empires of the Western Sudan that began around 1000 A.D., and the strengthening of cultural and commercial links across the Sahara with which this was associated,

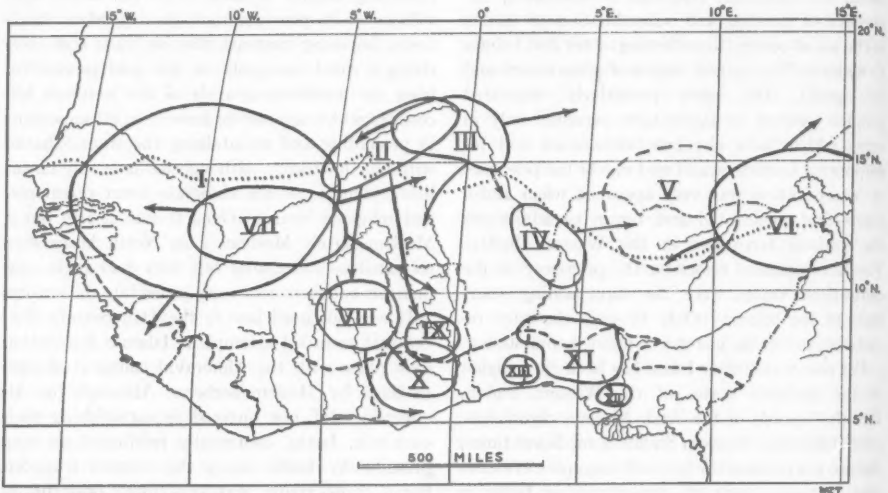

FIGURE 2. The orbits of early State systems of West Africa.
I. Ghana (4th C.? to 11th C. A.D.) and Mande (11th C. to 17th. C. A.D.)
II. Dja (? to 10th C. A.D.)
III. Songhai (9th C. to 16th C. A.D.)
IV. Kebbi (13th C.? to 18th C. A.D.)
V. Hausa States (10th C.? to 19th C. A.D.)
VI. Bornu (10th C.? to 19th C. A.D.)
VII. Bambara (17th C. to 19th C. A.D.)
VIII. Kumbu-Bona (Akan) (12th C.? to 16th C. A.D.)
IX. Bono (Akan) (12th C.? to 17th C. A.D.)
X. Asante (Akan) (18th C. to 19th C. A.D.)
XI. Yoruba (? to 19th C. A.D.)
XII. Benin (14th C.? to 19th C. A.D.)
XIII. Dahomey (Fon) (17th C. to 19th C. A.D.)

began early in the first millenium A.D. when the camel appears to have been first introduced from the east and established as the beast of burden in North Africa. Although they cannot yet be confirmed by archeological or ethnographic evidence, it is significant that the traditions of the older states of this wide zone all independently assert, as did those of Gana, that their founders were 'white' berber speaking peoples from the North. This holds for the Kingdom of Dja on the Niger bend which was disrupted and succeeded by the Songhai at the end of the first millenium A.D. when, significantly enough, the latter adopted Islam as the state religion. There are similar traditions in the later and mutilated chronicles of the Hausa states such as that of Kano which had widespread effects on the social systems and political forms, not least in assisting the rise to power of new centers and ruling groups. But it is clear that the impact of Islamic traders and teachers and later military forces from North Africa were not responsible for the first development of more productive crafts and agriculture, the specialization of occupations, the emergence of ruling aristocracies, of political centralization and administrative government. All these go back to a more remote period. Considerable chiefdoms had already been established early in the first millenium A.D. in the Western Sudan and the more successful expanded to form considerable empires.

On the other hand this cultural and political

development, whereby wide territories and large populations were organized and specialized crafts in metals, textiles and building developed, was clearly not a spontaneous development from small self-subsistent communities of primitive cultivators whose descendants survive in those parts of the Western Sudan, such as the south of Senegal, much of the Northern territories of the Gold Coast and the 'middle belt' of Nigeria which were never brought effectively within the orbit of the chiefdoms. To explain the emergence of the more complex cultures and political systems of the Sudan we have to seek the sources of their more elaborate crafts such as lost-wax casting in bronze and brass, filigree work in silver and gold, cotton weaving on narrow and broad looms, the construction of vaults and arches in adobe building; their possession of superior transport in the use of camels, horses and donkeys, and not least important their elaborate systems of belief in which the authority of king and chief is derived from their supernatural powers as the incarnation of gods.[5]

Fragmentary and little studied as is our knowledge of the rituals and cosmogonies of these early states and of their latter day successors it is clear that they belong to a tradition that is quite distinct from those of the clan-ancestor and earth cults of the kin-bound pagan communities. It has long been obvious too that many features of this tradition have close parallels in the beliefs and rituals of the ancient civilizations of the Levant. There the more advanced crafts found in the Western Sudan have a history extending back to the second millenium B.C. Since the Western Sudan is but the western segment of a habitable savanna belt extending east to the upper Nile and the Ethiopian highlands one might have expected that this would have provided a main route of cultural diffusion to the western lands south of the Sahara, more particularly since there were early chiefdoms and empires to the east between the Nile and Lake Chad as in Darfur and among the Baguirmi. But, up to the present, only meager and late indications have been found of cultural contacts with the old Nubian civilizations of the middle Nile. Such clues as we have point rather to indirect and intermittent traffic and incursions from North Africa into the Western Sudan by way of the oases of the Central and Western Sahara, and many of the recurrent elements have close parallels in the ancient civilizations of the Mediterranean and the Levant. How far back these trans-Saharan incursions go we do not know for our knowledge of the later prehistoric cultures of northern Africa is meager in the extreme. But it is clear that by the first millenium A.D. there were already considerable states strung out over the Western Sudan, that they traced their foundation to Hamitic speaking non-negroid invaders coming by way of the Saharan routes and oases.

The period of this development suggests the crucial importance of the introduction of the camel into North Africa which took place early in the first millenium and provided for the first time a riding animal and a beast of burden that could carry large bodies of men and goods across the waterless stretches of the desert.

Underlying the large scale organization and the widespread transport and exchange of goods in these early states of the Western Sudan was the possession not only of the camel, of key importance in more arid zones, but also of the horse and donkey. The horse, ultimately derived from S.W. Asia, was vitally important as a political and military instrument, for it made possible the concentration of military force at short notice against foot-bound peasantries, rapid communication of orders from capital to province, and the penetration of uncontrolled areas for slave raiding. Displays of horse riding on ceremonial occasions, the mounting with elaborate trappings of the chief and his emissaries which remain so characteristic today among all these peoples from the Mandingka to Bornu, are not meaningless ostentations, they remain symbols of authority expressed in what was once the key to power over this vast region.

The donkey as an economical beast of burden which could carry the loads of grain, raw materials and craft products from field to granary and market and from village to town and capital, afforded a great advance on human porterage. It may have been first domesticated in northeastern Africa but was not introduced into the Western Sudan until long after the first expansion of agriculture there.

It is with the more elaborately organized states too that the more advanced agriculture, the growing of cotton and the weaving of textiles is found. Voluminous tailored clothing in a Northern style, varying in elaboration and decoration according to rank contrasts strongly with the nudity of the pagan primitives outside the states.

Attention must also be called, in even the briefest survey, to the fact that a distinctive pastoral people is also widespread through the Western Sudan from Senegal to the Cameroons. Living

for the most part in small scattered communities this cattle keeping people, the nomadic Fula, are linguistically and racially distinctive. The main patterns of their culture and social life appear to be essentially the same over this vast range except where some groups have, from the 16th century onwards, dominated and later merged with the surrounding populations. Such Fula chiefdoms are known from the Lower Senegal river and the Futa Jallon highlands in the west to Northern Nigeria and the Cameroons. But the initial spread of the Fula peoples was not one of conquest. It was a much older dispersion of unobtrusive migrant cattle people living on the outskirts of the areas closely settled by cultivating peoples. Although often economically linked to these by an exchange of cattle for farm products they did not merge with them.

In language the Fula belong to one of the more northerly stocks of the West Atlantic group and have spread from the region of the Lower Senegal river. Their extensive and peaceful proliferation over the vast area extending eastwards for some 3000 miles must, as the closeness of their dialects shows, be comparatively recent but it appears to have been largely accomplished by the 15th century and may have long preceded the Islamicization of the Western Sudan. For the pastoral Fula have remained pagans and until the 18th century they actively resisted the encroachment of Islam, organizing opposition to it in many areas. The conditions that permitted these pastoral groups to expand so quickly and rapidly and to maintain their separate cultural identity are to be sought in the comparative stability and large scale organization of the early empires of the Western Sudan. It would appear that these migrant pastoralists were not only valued for their contributions to the economy but that their independence and freedom of movement was protected. Islam did not easily reach them and it was only when, in a remarkable *volte face* that some groups, beginning in the west in the late 17th century embraced Islam with fanaticism, that there developed the later Fula empires with which the French and British had to contend when they first sought to pacify and administer parts of the Western Sudan.

The essential features of the higer civilization of the Western Sudan, as it existed on the eve of Islamic penetration and persisted little changed under an Islamic veneer until the end of the 19th century, are even now only slowly being transformed under the impact of the railway and the truck, export crops and trade goods, European control and western administration.

This brief summary must not be taken to suggest that there was any sudden and wholesale imposition of an alien culture from across the Sahara. As in any other complex culture, there are all the marks of an amalgam built up over a long period, some of its elements in the ritual as much as in the technical sphere may be archaic, others late increments established in the Moslem period. Its particular configuration in any region varied considerably no doubt through time. Some features were more widely diffused than others. The dogmas of divine chieftainship with its attendant rituals could reach peoples like the Jukun of the southern savanna in Nigeria unaccompanied by substantial advances in crafts or new techniques of political control by a ruling class. Cotton growing and the loom could spread from the great states to surrounding peoples who knew nothing of divine chiefs or tribute to the state treasury. It was a slowly built cultural complex strongly established in some areas the elements of which spread unevenly over surrounding areas in the Western Sudan according to the vissicitudes of geography, cultural resources and human endeavor.

Incomplete as was the dispersion of these developments through the savanna belt of West Africa they were not confined to it. For the tropical rain forests to the south did not prove a complete barrier and at a number of points they penetrated deeply into it introducing new religious doctrines, sacred chieftainship, weaving and brassworking which were amalgamated in various ways with the archaic economy and social systems of this zone. But these introductions do not appear to have been effected by wholesale movements of population, for it is only exceptionally, as in the case of the Mende warrior chiefdoms of Sierra Leone, that northern language stocks have displaced the Kwa and other languages of the forest belt. Even where there have been profound modifications of social structure and great advances in craft and art one must look rather to the intrusion of small bodies of northerners who achieved dominance among pre-existing populations building up societies from which in turn others hived off to incorporate further groups in societies of similar pattern. Thus the Akan speaking peoples

of the Gold Coast and the Ivory Coast belong linguistically to the Kwa group but, as the records of early travelers confirm, were already organized in chiefdoms with an elaborate state ritual, highly developed crafts and capable of confederation into considerable states. And the Akan everywhere ascribe their origins, which does not necessarily mean the source of most of their populations, but that of their social system and sacred symbols, to a process of expansion and hiving off of state after state from ever farther to the north. In this way, as is now being shown in detail, the proliferation and expansion of Akan states can be traced back from the coast right through the forest belt to older communities in the southern savanna and these in turn have traditions of origins further to the north which point to the old kingdom of Dja that flourished on the Niger bend a thousand years ago.[6]

In southwestern Nigeria a series of chiefdoms also clearly deriving their impetus from some, at present unknown, northern focus developed among the Yoruba speaking peoples. Some were integrated prior to the 19th century under the powerful hegemony of Oyo, others proliferated more or less independently on the flanks to spread west into Dahomey and east among the Edo speaking peoples and the western Ibo as far as the Niger. To the north of the Yoruba on the edge of the savanna were other chiefdoms among the Nupe, Igala and other peoples that had existed long before the southward incursions of Moslem Fula who had, in the early 19th century, usurped control over the Hausa chiefdoms to the north.[7]

In addition to the development of major chiefdoms and the rise of centers of advanced crafts and elaborate art and ritual symbolism among such peoples as the Akan and the Yoruba, elements of this more complex civilization were introduced piecemeal over the centuries among other peoples so that its pale reflection is found in small epigonal communities. It is as far a cry from the 17th century capital of the King and Queen Mother of Bono, with its mile long avenues, elaborate court ritual and wealth of gold and silver ornaments to the petty chieflets of the Ewe in Togoland as it was from the court of the Alafin of Oyo, before the Fulani raiders disrupted his empire, to the priest chief of Nri among the Northern Ibo. But all belong to the same ferment that was still spreading through the West African forest zone when Europeans first appeared on the surf-beaten coast to introduce new and powerful cultural forces.

The techniques and skills, whether in craft or social organization, that are characteristic of the main centers of cultural development in the forest belt, as among the Akan and the Yoruba, present a remarkable contrast to those of autonomous village communities remote from such centers. Cotton is grown for weaving; the high status of chief or official is marked by the wearing of long robes and elaborate head gear; precious metals and stones are elaborately fabricated for decoration; the technique of casting bronze and brass is elaborated for ceremonial objects; man-power is organized to build elaborate courts and to raise armies for conquest and defense, towns are protected by encircling ditches and walls and defended gates. Despite the hazards of infection in the tsetse ridden bush and forest, the Yoruba succeeded in rearing horses for use by chiefs and officials, in ceremonials and not least in war. Although the diffusion of some crafts and customs to some surrounding peoples produced cultural gradations of many kinds, the technically elaborate culture and the centralized social systems of such peoples contrast strongly again with those of such forest peoples as the southern Ibo of Nigeria or the tribes of the western Ivory coast and Liberia to whom such things remained quite unknown.

The establishment of European trading posts along the Guinea coast introduced not so much new knowledge as opportunities to acquire a few vitally important supplies which in some regions profoundly affected indigenous political relations in the hinterland. Of the western goods the traders offered the most portentous were muskets and gunpowder. These, combined with the European demand for slaves, put a premium on militarization. Slavery and slave raiding was almost certainly already established on a considerable scale in the larger states of the forest belt. Slave raiding and trading now became the means whereby the new instruments of dominance and empire could be obtained. But the coast had hitherto offered little attraction to the rulers of the larger chiefdoms. These had looked northward to traffic with the Sudan. Thus old Oyo, the capital of the paramount chiefdom among the Yoruba down to the 18th century was 200 miles inland as were Bono and Bona the largest and wealthiest chiefdoms of the Akan in the 16th

century and those to which the lesser states nearer the coast traced their origins. Unexpected opportunities were offered to leaders among the coastal peoples to build up trading empires. Where a state system already existed as among the coastal Akan this provided the framework within which, with increasing militarization of organization, they sought to obtain slaves by raiding and to defend local monopolies over the supplies of guns and powder that offered so unexpected a means to wealth and power. In the same way petty coastal chiefdoms among the Yoruba rose to influence in the new traffic with the interior. But the inland states were also driving for direct access to the European trading posts and control of routes through the forest. It was in this way that, after many vicissitudes between warring states, the minor and recent Akan state of Kumasi broke the power of its great neighbors Denkyera to the south and Bono to the north and by overawing others, created and dominated the confederacy of Ashanti in the 18th and 19th centuries. So, too, a succession of rulers of a petty state among the Foñ were able from small beginnings at Abomey to build up one of the most remarkable chiefdoms of the forest belt. Dahomey, with its combination of elaborate state ritual that combined traditional features of sacred chiefship with military leadership, political despotism, complex business administration of plantations, trade and markets, and its organization of slave raiding and warfare, was a response to the unique opportunities that European trade provided. The story of the rise of the Kingdom of Benin in the forests west of the Niger follows a similar pattern. In nearly all cases these strong chiefdoms of the forest belt resisted by force later European attempts to penetrate and control the interior and their power could only be broken by war.

Where the coastal peoples were, at the time of European contact, still dispersed in small communities and out of range of inland states, they responded by developments consistent with their earlier social systems. Local kin groups built up bodies of slave dependents to man trading and war canoes and monopolize rivers and creeks that gave access to their neighbors and opportunities for raiding and trading. In this way, for example, the coastal Ibibio built up at the mouth of the Calabar river and in the Delta of the Niger, settlements controlled by rival bodies of kinsfolk which organized the traffic in slaves and later in palm oil with the hulks of the Europeans moored alongside. So grew up the wealthy 'Houses' of Calabar in the 18th and 19th century and the shortlived commercial dominance of Jaja at Bonny at the end of the last century. From such trading centers the impact of commerce on the coast spread back to the interior. Participation in the trade in slaves and later oil provided a means of securing guns and powder, of raiding instead of being raided, promoting the rise of petty war leaders with their personal followings and their new patterns of prestige at the expense of the traditional authority of the elders of lineages and the priests of the local shrines.

But direct European influence did not begin to penetrate into the forest belt until the end of the 19th century and the grasslands were almost completely cut off from it except in the far west where they extended to the sea in Senegal. Thus the missionary and educational influences, the beginnings of western literacy and the participation in overseas commerce which began to be significant on the coast from the middle of the nineteenth century remained insignificant in the western Sudan until after the first world war. This immense contrast between the coast and the grassland interior of West Africa in the period over which western ways and resources became gradually more familiar and acceptable is often forgotten in appraisals of the economic and political situation in West Africa today.

The old cultural forms and social systems of West Africa are now being eroded and superseded at an ever-increasing rate as its peoples are, often at their own vigorous insistence, being incorporated economically and ideologically into the modern world and are being reorganized domestically and politically along Western lines. In relation to the pace of cultural and social transformation that is taking place today the amount of research into the traditional patterns of life has been and still is pitifully small. Those who recognize that a deeper understanding of the cultural history of man, and of the processes underlying the variety of socio-cultural patterns, depends in large measure in recording and analyzing as fully as possible, with the tools of modern anthropology, the ways of life of non-western peoples; those who recognize that knowledge of the background and past of a people is a powerful aid to constructive cooperation with them, should also understand that unless far more resources are devoted to training and

financing field research and comparative study of these West African peoples over the next twenty-five years the opportunity will be for ever lost. For, unlike the biologist who can still count on finding many older forms of life surviving for investigation, the anthropologist is only too clearly aware that the socio-cultural plasticity of Man is such that an ancient cultural pattern or a social system can disappear virtually without trace over a few generations.

This has been in part my reason for attempting in a brief address the overbold task of sketching, from woefully incomplete knowledge, what seem to me to be some of the outstanding phases of the cultural development of West Africa and to suggest the ways in which the broad factors in the natural environment combined with a succession of external stimuli and local responses have contributed to the complexity and variety of the cultural map of West Africa. That I have oversimplified I know; that I have entertained historical connections or adaptive relations which cannot be substantiated on present knowledge I recognize. But a useful purpose in the field of scholarship and cultural understanding will have been served if I have been able to point to some of the probabilities and possibilities in this field and to show that these are a challenge to more intensive and systematic inquiry while there is yet time to study the native cultures of West Africa that have survived into the modern world.

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DIVISION OF MYCOLOGY

UNUSUAL MYCOSES CAUSED BY UNCOMMON OR RARE FUNGI*

By MORRIS MOORE†

Although well over a century has passed since medical mycology first became noticed as an important adjunct to applied medicine, much information concerning both the clinical and mycological aspects is yet to be acquired. In fact, much new data have been gathered within the past thirty years. Yet, there is a great deal more that can be learned by those eager and willing to apply themselves and for the student of mycology this particularly has reference to the physiology and taxonomy of the pathogenic fungi. For the clinician, and for those mycologists who are in contact with the patient, the opportunity for gathering newer or unusual details of the clinical manifestations of mycoses caused by rare or uncommon fungi should not be overlooked.

The following cases are being presented due to first the rarity with which the causative fungi are found and, secondly because of the unusual lesions produced.

Onychomycosis Caused by Hyalopus sp. *and* Syringospora (Monilia, Candida) Parapsilosis

The first case is that involving the nails of a young white girl who was first seen when she was 14 years of age. The nail lesion of the left thumb started as a yellowish-blue spot which then became yellow. Treatment with soaks and topical application of iodine caused the nail to peel repeatedly and to become quite thin. The disease spread to the nails of the second and third fingers. Following continued treatment with X-rays the nails appeared to become clear.

Cultures and potassium hydroxide (30 per cent) preparations were made from the involved thumb nail. In the smears there were found clumps of yeastlike, budding cells and branching chains of cells. In addition, there were large clumps of intertwined filaments showing thick-walled, elongate and short, irregular cells and numerous round, thick-walled cells.

* This paper, illustrated with lantern slides, was presented at a meeting of the Section on March 27, 1953.

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Primary cultures were obtained from nail scrapings on Sabouraud's glucose agar. Discrete to confluent colonies of the yeastlike organism were found and in addition, a grayish mycelial mat developed which then became salmon colored. On subculture, these were identified as *Syringospora* (*Monilia, Candida*) *parapsilosis* and *Hyalopus* (*Cephalosporium*) unidentified species.

Mycology. Subcultures of the *Hyalopus* species were made on various mycologic mediums. On Czapek's agar there developed a flat, arachnoid colony measuring 7 cm. in diameter after 7 days, with a central rose-colored zone and a grayish periphery. On Sabouraud's glucose agar, after 7 days, there was formed a cottony colony showing concentric rings of growth. The color, at first grayish, became yellowish then dark salmon and finally brownish salmon or reddish-brown. On potato-dextrose agar, the colony was flat and smooth, showing sectoring. The colony was 7.2 cm. in diameter after 7 days and the color also was a pinkish-brown.

Measurements of the mycelial elements showed that the hyphae were 2–6 microns in diameter; hyphal cells, 4–6 by 8–10 microns; chalmydospores, 6–9 microns in diameter with some measuring up to 15 microns; conidial heads, 15 by 18 microns; conidia, 3–4 by 7–15 microns. The germinating conidia developed thick walls showing a central indentation and finally developing a single septum.

Carbohydrate reactions. Glucose and sucrose showed slight acidity whereas maltose, lactose, levulose, galactose, dextrin and inulin became alkaline.

Litmus milk was not coagulated or acidified. Gelatin was not liquefied.

Classification. According to Dodge[1] the genus *Hyalopus* was created by Corda in 1838 and in the following year he created the genus *Cephalosporium*. It is felt by many that the genera actually are synonomous and that *Hyalopus* has preference. The genus *Cephalosporium*, however, has been used more widely and consequently is more familiar.

A number of species have been described as pathogenic. These have been isolated from varied lesions including mycetomas, onychomycosis, eczematoid skin and scalp lesions, gummatous and verrucous or ulcerous skin lesions, keratomycosis of the eye, mucous membrane lesions, interdigital eruptions and dermatomycosis of the *Trichophyton* and *Epidermophyton* types. It seems as though whenever a strain has been isolated it has been described as a new species. Undoubtedly many of the species were involved as pathogens, however, since some strains were not demonstrated in the infected tissue there is some doubt as to their pathogenicity. At the present time, approximately 18 strains have been described as species of *Hyalopus* (*Cephalosporium*).

Barbosa[2] in 1941 reviewed the species of *Cephalosporium* and *Hyalopus* and combined them in the one genus *Hyalopus*. He further divides the genus into subgenera based on whether yeast cells are or are not present in culture, and whether the germinating conidia are unicellular, uniseptate or multiseptate.

According to this classification, the organism described from the patient reported here would fit into the subgenus *Maffiella Ciferri*, where the conidia have a single septum. Here Barbosa lists two species. The first and type species is *H. serrae* which produces rose-colored colonies with conidia measuring 4–8 by 3–4 microns. The second species is *H. keratoplasticum* described by Morikawa in 1939[3] from verrucous lesions of the foot and toes.

H. keratoplasticum has branching septate mycelium with the hyphae measuring 1.5–4.5 microns in diameter. Terminal or intercalary chlamydospores measure 3–8 microns. The conidiophores are short, simple, non-septate, lateral formations measuring 10–50 microns. The conidia are smooth, oval or elliptical, measuring 7.5–13 by 3–4 microns, forming a single medial septum. The organism ferments maltose and mannose slightly and does not affect glucose, lactose, levulose arabinose, dextrin, inulin and mannite.

Litmus milk was not coagulated and gelatin was not liquefied.

With the exception of some minor differences in gross cultural characteristics and in the carbohydrate reactions, the organism described in this paper has much in common with *H. keratoplasticum*.

Nocardiosis *of the Knee*

The second case is that of a 49 year old white man who developed a lesion of the left knee. The history of the lesion was indefinite although he remembered bumping the knee on the edge of his metal desk.

When originally seen, the involved area was coin-shaped, blue in color, consisting of several closely packed nodules and measured 2 cm. in

diameter. Cultures were negative and biopsy material sent to three different dermal pathologists was not definitely diagnosed.

Following X-ray therapy, without any sign of improvement, the patient was referred to St. Louis for consultation purposes. At this time the lesion had increased in size to 2.0 by 3.5 cm. The involved area now included two groups of raised, scaly, closely packed subcutaneous papules with hemorrhagic centers.

Smears made from the hemorrhagic centers revealed yellowish-white clumps of mycelium. Cultures made from the same material developed small, discrete, creamy-white colonies on the fifth day, on Sabouraud's glucose agar, which were identified as a species of *Nocardia*.

Pathology. The histologic picture of sections of tissue was that of an acute to chronic inflammatory process with the characteristic infiltrate. Macrophages were present, some filled with blood pigment. Giant cells were also numerous. There were many microabscesses both in the cutis and in the epidermis and in many of these there were variously shaped masses of filaments and coccoid bodies. The organism was not acid-fast, although the gloea-like substance surrounding the mycelial clump did stain with carbol fuchsin.

Mycology. The organism was subcultured on various mediums. Growth was good at both room temperature and 37° C.

In glucose-peptone broth, a pellicle formed on the surface which was wrinkled and yellow-orange or ochraceous-orange in color. On Czapek's medium growth was poor, showing a yellow colony, 0.5 cm. in diameter after 35 days. On Sabouraud's glucose agar the colony was approximately 1 cm. in diameter after 22 days, vermiculate in appearance and yellow-orange in color with a creamy-white pubescence. Individual colonies were mammiliform to crateriform, measuring approximately 2-3 mm. in diameter after 35 days. On potato-dextrose agar the colony was vermiculate, ochraceous-orange with a creamy-white periphery, with a brownish discoloration of the medium and measured 1.5 cm. in diameter after 28 days. The organism grew better on glycerinated medium and on glucose agar plus 1 per cent yeast extract. On beef extract agar growth was good with a brownish discoloration of the medium. The fungus grew well on both carrot and potato plugs with or without glycerin. When glycerin was used, the colony developed a creamy-white aerial growth. On blood agar growth was good and there developed a zone of hemolysis around the colony.

The cultures gave off a distinct moldy or earthy odor which was not lost on repeated subculture.

Serum was not liquefied. Starch was not affected. Gelatin liquefied slowly beginning on the surface and the medium developed a brownish discoloration. Paraffin was utilized as a sole source of carbon. Phenol was not tolerated.

Litmus milk was not acidified or curdled. The organism developed as a yellowish-orange growth at the bottom of the tube. On the surface there were discrete, minute, grayish colonies. Smears made from the litmus milk growth stained by the Ziehl-Neelsen method revealed some acid-fast filaments and coccoid bodies.

Microscopically the organism showed fine filaments with alternate branching developing at right angles. The filaments broke up into bacillary forms and also developed terminal chains and then clumps of ovoid to coccoid, intensely staining bodies. Some of the terminal cells showed clubbing.

Classification. The classification of this organism presented a problem when first isolated. Grossly it had the characteristics of *Nocardia asteroides*, both as to color (yellow to ochraceous-orange) and colony markings. However, the organism was not acid-fast in tissue as is characteristic of *N. asteroides*. In a review of the literature it became evident that this strain of *Nocardia* had much in common with *N. (Actinomyces) mexicana* described by Boyd and Crutchfield.[4] A further review revealed that *N. mexicana* is considered by Ochoa[5] to be synonomous with *N. brasiliensis*, reported by Lindenberg in 1909.[6] *N. brasiliensis*, on the other hand, is considered by some to be in synonomy with *N. asteroides*.

In 1841, de Almeida and Lacaz[7] compared *N. brasiliensis* with *N. asteroides* and concluded that they were distinct species. They describe *N. brasiliensis* as gram-positive and showing microscopically long, rectilinear or spiral branching filaments which fragment and form coccoid bodies. In milk the filaments are acid-fast. This latter observation, first made by Lindenberg, is apparently why the organism is included among the acid-fast *nocardias*. The organism isolated from the patient reported here likewise formed acid-fast filaments and coccoid bodies in litmus milk. However, the fungus was distinctly not acid-fast in tissue. Actually, there is insufficient evidence to

warrant considering *N. brasiliensis* as an acid-fast organism since it has been shown that non-acid-fast bacteria may develop acid-fastness when grown in milk.

According to the description of *N. brasiliensis* and its synonym, *N. mexicaca*, by Conant and Rosebury,[8] then the organism reported here would be *N. brasiliensis*. However, the acid-fastness should be considered as present only in milk as originally described. Undoubtedly there are strain differences both as to color and biochemical properties.

It is of interest also that the first case described by Lindenberg, caused by *N. brasiliensis*, had lesions of the knee, thigh and leg. Several cases have been mycetomas. In 1935, de Almeida[9] reported a knee lesion very similar to the one described here and caused by the same organism.

Mycetoma of the Hand and Arm

The third case is that of a 64 year old colored man, a cotton picker, who had lived on farms in Mississippi and Missouri all his life. He was referred to Barnes Hospital with a complaint of a swollen and painful right arm.

Fifteen years previously he had noticed a small, non-tender, freely movable smooth nodule in the skin over the outer surface of the right wrist. The swelling and pain subsided and reappeared alternately for the next seven years. He did not recall any trauma to the original site. The nodule, however, became progressively larger and after the seven year period it burst and exuded hard black "bird-shot" material. A few days later several small tender sores were noted around the wrist and these, which when they ruptured, exuded the same black, hard material. The arm became swollen and tender. The number of nodules increased over the next few years to involve the entire forearm and much of the hand. The involved area became extremely hot to the touch and there developed a stiffness of the elbow, wrist and finger joints. Because this interfered with his cotton picking he went to his physician who treated him with 1,200,000 units of penicillin. Failing to respond to this therapy, he was referred to the U. S. Public Health Service in St. Louis to rule out syphilis. He was then referred to Barnes Hospital for further examination and diagnosis.

A roentgenogram of the hand and arm showed soft tissue deformity and changes in the carpal bones which suggested the possibility of osteomyelitis.

Smears made from the draining sinuses showed black granules composed of fungus filaments and spores. Cultures were made on Sabouraud's glucose agar. On the third day there developed a grayish growth of filaments which a few days later became light yellow and then yellowish-brown with a brown discoloration diffusing into the substratum. The organism was identified as a species of *Madurella*.

In spite of adequate, diverse treatment, there was no improvement, and the arm was removed by supracondylar amputation.

Pathology. Grossly, the amputated arm and hand showed numerous sinuses. On sagittal section, the bones of the wrist, especially the hamate bone, were found to be involved as well as the bones of the hand. Dark brown granules were found in globular, discrete masses extending through the epidermis and in confluent sinus tracts.

Microscopically, the tissue showed advanced fibrosis and chronic inflammation around masses of the organisms which were dark brown in color. The masses were made up of chlamydospores measuring 6–12 microns in diameter and thick, short filaments. The inflammatory process was characterized by numerous new capillaries, plasma cells, scattered polymorphonuclear leucocytes, eosinophils and small round cells. There were many fibroblasts and foam cells, many of the latter engulfing brown pigment globules. The reaction involving the fungus was of two types. In the early stage the fungus, consisting of filaments only, was surrounded by giant cells of the foreign body type chiefly, some polymorphonuclear leucocytes and fibroblasts. The second type or stage is concerned with the mature fungus granule which is made up of large, spherical, thick-walled cells, the chlamydospores, and short filaments. Now there are present many polymorphonuclear leucocytes surrounding the fungus granule. This was all encapsulated by a zone of fibrous tissue or fibrous connective tissue.

Mycology. Subcultures were made on various mediums. Growth was best at 37° C.

On conservation agar the colony was arachnoid in appearance, gray in color with numerous pinpoint sized black sclerotia over the surface. There was some brownish discoloration of the medium. On Sabouraud's glucose agar growth was poor, the colony being acuminate, cerebriform and yellowish-brown to dark chamois in color. No sclerotia were seen. On potato-dextrose agar the growth

was arborescent and gray, then grayish-brown in color. Numerous large, black, irregular sclerotia were present in the central zone. On corn-meal agar the growth was mostly submerged in the medium and showed diffusible brown pigment; scattered sclerotia could be seen throughout the growth both in the deep and superficial portion of the medium. On Czapek's agar the growth was submerged and visible with transmitted light. Sclerotia were pin-point in size and scattered throughout the entire central area. In broth, large floccules developed on the bottom of the flask.

Starch agar developed deep brown colonies and the starch was hydrolized. Gelatin was not liquefied. Litmus milk was not acidified or curdled. Serum (inspissated) was not liquefied.

Microscopically, the hyphae varied in diameter from 1–6 microns, usually 2–5 microns. The hyphae were long and thin or short and thick. Oidioid or moniliform cell formation (some dumbbell shaped) was noted, the cells measuring from 6–9 microns in length, some longer. Oidia measured 6–9 microns. Chlamydospores, lateral, intercalary or terminal, varied considerably in diameter from 6–27 microns. Many measured 12–15 microns while the large ones measured 22–27 microns. Sclerotia varied from 0.5–1 mm. in diameter, the mature forms showing a wall made up of uniformly thick-walled cells measuring approximately 8 microns in diameter.

Classification. The classification of the species of *Madurella* is still in a state of confusion. The genus was created by Brumpt[10] in 1905 using as his type species, Streptothrix mycetomi of Laveran.[11] The species and genus were based on the observation of the granules in tissue rather than on cultures. Consequently, the name was considered as a *nomen dubium* by Vuillemin[12] and others.

In 1911, both Chatterjee[13] and Brault[14] isolated and described what they considered to be *M. mycetomi*. In 1912, Brault[15] enlarged upon his original description. In 1918, Puyhaubert and Jolly,[16] in 1920, Yazbek[17] and in 1922, Noc and Jouenne[18] published detailed description of what they considered to be *M. mycetomi*.

It is difficult to know whether these investigators were dealing with the same species or with strains of different species since there are some differences and secondly the original cultures are no longer available.

In 1926, Gammel, Miskdjian and Thatcher[19] described *M. americana* and in 1927, Gammel[20] described *M. ikedai* as new species. In the latter publication Gammel reviewed the descriptions of *M. mycetomi* and concluded that his two species were different from *M. mycetomi*.

The organism isolated from the case reported here agrees with that described by Gammel as *M. ikedai*, in many respects. In a personal communication, Gammel believes now that both *M. americana* and *M. ikedai* are strains of the same species, *M. americana*. According to the descriptions of *M. mycetomi* by Yazbek, Noc and Jouenne, Brault and others, it is quite probable that *M. americana* may be similar to *M. mycetomi*. This is the opinion of MacKinnon.[21] A strain of *Madurella* designated as *M. americana* now in the collection of several mycologists does not conform to the original description by Gammel. Gammel further believes that that is not the organism described and distributed by him.

The classification of the genus *Madurella* is greatly in need of reevaluation. Negroni, Fernandez and Daglio[22] grouped the species on the basis of gross cultural characteristics. These features, however, are variable within strains and thus should not be relied upon completely. Ciferri and Redaelli,[23] on the other hand, combined the genera *Madurella* and *Indiella* in the one genus *Madurella*. They further created subgenera based on color and whether the granules are present in tissue alone or in tissue and in culture mediums. These too are not entirely reliable as characteristics since they may well vary from one strain to another. Of the number of species created, some may be synonomous with others, and some as *M. (Rubromadurella) langeroni* are untenable since the organism was never cultured.

This case represents the fourth mycetoma of the hand and/or arm caused by *Madurella*, in the available world literature, and the first in a native of the United States.

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NOTICE TO ACTIVE MEMBERS

In accordance with the Bylaws of the Academy, Article VII, Section 7, the Nominating Committee of the Council is inserting in this April issue a notice to Active Members, quoting Article IV, Section 1 of the Bylaws.

Article IV, Section 1 reads as follows:

"*Suggestions by the Members for Nominations.* Suggestions for nominations of Officers of the Academy and Members of the Council, with the exception of Sectional Chairmen, may be sent in writing by any Active Member of the Academy, addressed to the Nominating Committee of the Academy, 2 East Sixty-third Street, New York, N. Y., with the name of the proposer. To be considered, such suggestions must be received not later than September first of each year."

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Elected March 26, 1953

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Barbieri, Delfino, Ematolgia. Assistente di ruolo presso la clinica Medica Generale dell'Universita di Milano, Milan, Italy.

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